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MORPHOLOGICAL AND ANATOMICAL OBSERVATIONS ABOUT *MARILIASUCHUS AMARALI* AND *NOTOSUCHUS TERRESTRIS* (MESOEUCROCODYLIA) AND THEIR RELATIONSHIPS WITH OTHER SOUTH AMERICAN NOTOSUCHIANS[1]

(With 19 figures)

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ABSTRACT: The phylogenetic relationship of the notosuchians *Mariliasuchus amarali* (Campanian; Bauru Group) and *Notosuchus terrestris* (Santonian; Neuquén Group) is revised. Morpho-anatomical evaluation of *Mariliasuchus* in the current bibliography indicate close relationship with *Notosuchus*, while cladistic analysis either related *Mariliasuchus* to *Candidodon itapecuruense* (Albian/eo-Cenomanian; São Luis-Grajaú Basin), as part of the phylotaxon Candidodontidae, or to *Comahuesuchus brachybuccalis* (Santonian; Neuquén Group). Comparative study of specimens shows similarities on the palate, choanae, dentition, retroarticular process, and other structures from *Mariliasuchus* and *Notosuchus*, supporting the original classification as a Notosuchidae. Preliminary phylogenetic analysis sets these taxa as sister-groups. Reevaluation of a previously published phylogenetic analysis from other authors provides further support for the *Mariliasuchus*+*Notosuchus* clade. The current work indicates that *Mariliasuchus* is a Notosuchidae, refuting its allocation as a Candidodontidae. The influence of character construction and the definition of Notosuchia are discussed.

Key words: *Mariliasuchus*. *Notosuchus*. *Candidodon*. Notosuchia. Cretaceous.

RESUMO: Observações morfológicas e anatômicas sobre *Mariliasuchus amarali* e *Notosuchus terrestris* (Mesoeucrocodylia) e suas relações com outros notosúquios sulamericanos.

As relações filogenéticas entre os notosúquios *Mariliasuchus amarali* (Campaniano; Grupo Bauru; Brasil) e *Notosuchus terrestris* (Santoniano; Grupo Neuquén; Argentina) são revisadas. A avaliação morfo-anatômica de *Mariliasuchus* na bibliografia corrente indica parentesco próximo com *Notosuchus*, enquanto análises cladísticas tanto relacionam *Mariliasuchus* a *Candidodon itapecuruense* (Albiano-eo-Cenomaniano; Bacia de São Luis-Grajaú), como parte do táxon Candidodontidae, ou com *Comahuesuchus brachybuccalis* (Santonian; Grupo Neuquén). Estudo comparativo de espécimes traz novas informações sobre palato, coanas, dentição, processo retroarticular e outras estruturas de *Mariliasuchus* e *Notosuchus*, suportando a classificação original como Notosuchidae. Análise filogenética preliminar posiciona estes taxons como grupos-irmãos. Reavaliação de análise filogenética previamente publicada por outros autores fornece evidência adicional para um clado *Mariliasuchus*+*Notosuchus*. O trabalho presente indica que *Mariliasuchus* é um Notosuchidae, refutando a sua alocação em Candidodontidae. A influência da construção de caracteres e a definição de Notosuchia são discutidas.

Palavras-chave: *Mariliasuchus*. *Notosuchus*. *Candidodon*. Notosuchia. Cretáceo.

INTRODUCTION

The Cretaceous of South America is rich in many species of fossil crocodylomorphs, especially the Mesoeucrocodylia (Bertini, 1993; Bertini *et al.*, 1993; Bertini & Carvalho, 1999; Kellner & Campos, 1999; Carvalho & Bertini, 2000; Leanza *et al.*, 2004; Andrade, 2005; Candeiro *et al.*, 2006). Among the South-American forms, several fossil taxa constituted highly adapted terrestrial crocodylians, with lateral orbits

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and oreinrostral snout (*e.g.*, *Araripesuchus, Lomasuchus, Peirosaurus*), frequently showing short rostrum and specialized dentition (*e.g.*, *Candidodon, Comahuesuchus, Uruguaysuchus*). *Notosuchus terrestris* and *Mariliasuchus amarali* are two special examples of Mesoeucrocodylia, sharing several characteristics with each other (*e.g.*, maxillo-palatine fenestrae, single terminal nares, elongated glenoid fossa, triangular choanae, fenestrated quadrate). They are usually referred as notosuchians, although definition of this group has been extensively debated (Gasparini, 1971; Buffetaut, 1981, 1982; Benton & Clark, 1988; Clark, 1994; Ortega *et al.*, 2000; Sereno *et al.*, 2001; Andrade, 2005; Zaher *et al.*, 2006) and divergences on its composition and range occur. *Notosuchus* and *Mariliasuchus* are among the most common fossil crocodylians from Argentina and Brazil respectively, with several specimens collected. Nevertheless, only a fraction of the specimens from both taxa were properly described (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Carvalho & Bertini, 1999; Zaher *et al.*, 2006). Though both *Mariliasuchus* and *Notosuchus* were previously related to other notosuchians in morpho-anatomical studies, their close phylogenetic relationship has not been always recognized. The objective of this paper is to compare morphological features of *Notosuchus terrestris* and *Mariliasuchus amarali*, discuss some of the characters uniting these notosuchians and explore the relations of these species with other South American notosuchians.

THE FOSSIL CROCODYLIAN *NOTOSUCHUS* FROM PATAGONIA

Notosuchus terrestris Woodward, 1896 (Fig.1) is one of the first species of fossil crocodylomorphs to be described from South America, which was the focus of many studies during the last century (Woodward, 1896; Saez, 1957; Gasparini, 1971; Bonaparte, 1991; Pol, 1999, 2005; Martinelli, 2003; Andrade, 2005; Fiorelli, 2005; Andrade *et al.*, 2006). Several specimens, from the Upper Cretaceous of the Neuquén Basin, Bajo de La Carpa Formation, are distributed throughout paleontological collections from Argentina, such as MACN, MLP, MUCPv-UNC/"Proyecto Dino" and MPCA. The material available includes cranial and postcranial remains, composing an impressive group of more than 40 specimens, all from Patagonia (Argentina). There are several reconstructions of *Notosuchus terrestris* available from published works, where different interpretations show the lack of consensus on the morphology of the species (Fig.1).

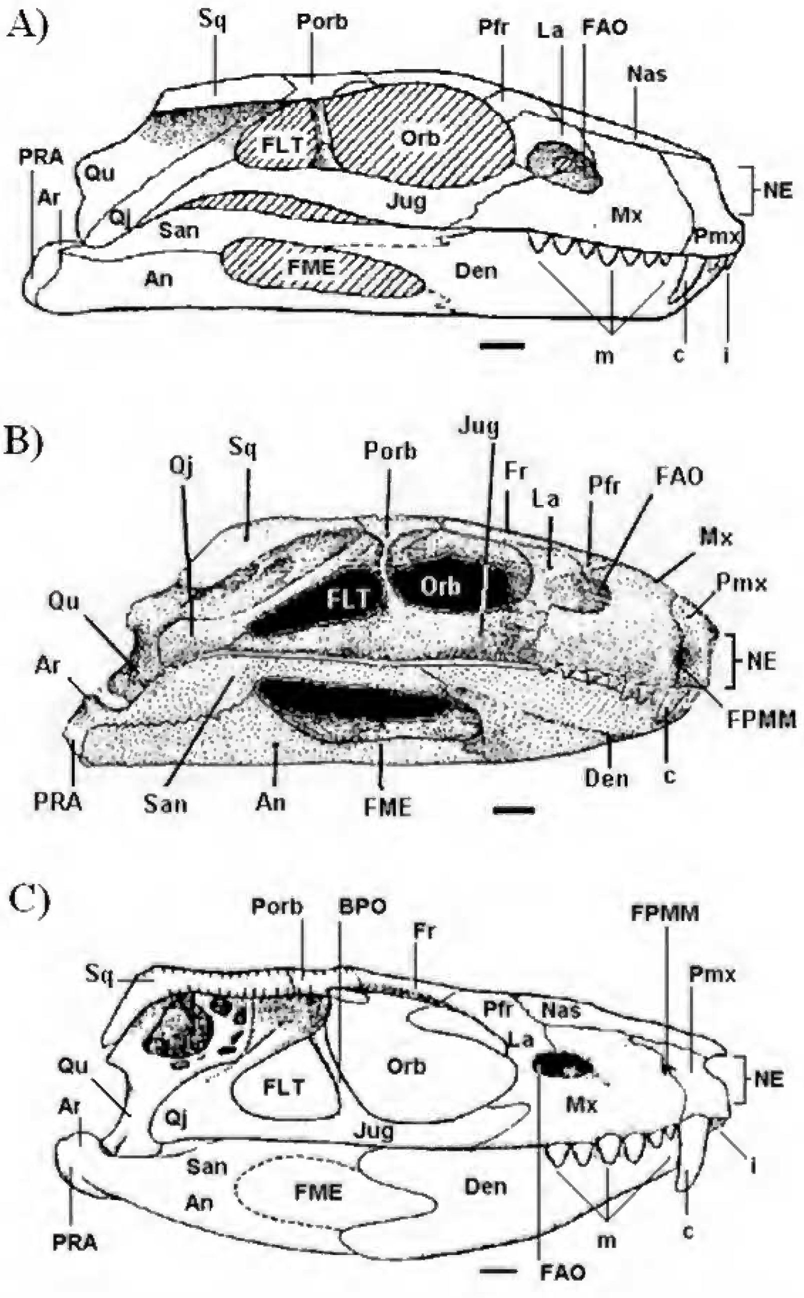

Fig.1- *Notosuchus terrestris*, as reconstructed by different authors; A) reconstruction based on MLP 64-IV-16-5, lectotype, from Price (1959); B) reconstruction based on MLP 64-IV-16-5, from Gasparini (1971); C) reconstruction based on the MACN-Pv-N specimens, from Bonaparte (1991). Note the differences on the reconstruction of the rostral region, antorbital fenestra, dentition, quadrate surface, general morphology of the mandible and retroarticular process. Bar = 10mm.

The Family Notosuchidae Dollo, 1914 was originally erected to *Notosuchus terrestris* alone, defined then as a Mesosuchia Huxley, 1875. The new species was very different from any other known fossil crocodylomorph described until the first half of the Twentieth Century. A second species, *Notosuchus lepidus*, was posteriorly described by SAEZ (1957) based on two poorly preserved specimens (MLP 64-IV-16-1, MLP 64-IV-16-2), which was subsequently considered as a junior synonym to *N. terrestris* by GASPARINI (1971). The work of GASPARINI (1971) extended the observations on *Notosuchus* and included the genus in the Infra-Order Notosuchia, along with *Araripesuchus* and *Uruguaysuchus*. In this work, specimens from the original collection of the La Plata Museum were reorganized and a new number assigned to them. GASPARINI (1971) also elected a lectotype for *N. terrestris*, as the original description referred to the specimens as a group.

The development of the cladistic methods allowed a revision of general phylogenetic relationships, and works ranging main groups of crocodylomorphs (BENTON & CLARK, 1988; CLARK, 1994) assigned *Notosuchus* to the Mesoeucrocodylia. BONAPARTE (1991) described additional materials in detail (MACN–Pv–N–22, MACN–Pv–N–23, MACN–Pv–N–24), providing valuable information on the species. Based on the structures of the basicranium and the perforated quadrate, BONAPARTE (1991) suggested that *Notosuchus* could be related to the protosuchian lineage. Even though there is a huge variation upon the topologies obtained for Crocodylomorpha (WU *et al.*, 1995; WU & SUES, 1996; GOMANI, 1997; POL, 1999, 2003, 2005; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; MARTINELLI, 2003; SERENO *et al.*, 2003; CARVALHO *et al.*, 2004; POL & NORELL 2004a, 2004b; ANDRADE, 2005; FIORELLI, 2005; FIORELLI & CALVO, 2005; POL & APESTEGUIA, 2005; TURNER & CALVO, 2005; JOUVE *et al.*, 2006; TURNER, 2006; ZAHER *et al.*, 2006; LARSSON & SUES, 2007; LAUPRASERT *et al.*, 2007), all subsequent phylogenetic studies support *Notosuchus* as a Mesoeucrocodylia. Substantial new information was provided by POL (1999, 2005), who contributed to the understanding of *Notosuchus* describing new postcranial remains (MACN–Pv–RN–1037), showing the relevance of this type of data for the study of crocodylomorph evolution. Furthermore, several other specimens exist, as reported by the unpublished works of ANDRADE (2005) and FIORELLI (2005), providing a huge amount of new and important data.

Phylogenetic relationships proposed and published for *Notosuchus terrestris* relate the species to several other notosuquians and sebecosuchians, in a series of different hypothesis, most of them supported by only a few other works. Closer relationships with other notosuchians include *Malawisuchus mwakasyungutiensis* Gomani, 1997 (as in WU & SUES, 1996; GOMANI, 1997; SERENO *et al.*, 2001, 2003; LARSSON & SUES, 2007; LAUPRASERT *et al.*, 2007), *Sphagesaurus huenei* Price, 1950 (as in MARTINELLI, 2003) and *Uruguaysuchus* (as in JOUVE *et al.*, 2006). It is also related to comahuesuchids (TURNER, 2004, 2006; TURNER & CALVO, 2005), although these authors included *Anatosuchus* in this clade (as in SERENO *et al.*, 2003; *contra* MARTINELLI, 2003; ANDRADE *et al.*, 2006). A closer relationship with sebecosuchians is presented by ORTEGA *et al.* (2000) and CARVALHO *et al.* (2004), where *Notosuchus* is depicted by as the basalmost Ziphosuchia, along with *Libycosuchus*, baurusuchids and other sebecosuchians.

Other different hypothesis includes mixed relationships with notosuchians and sebecosuchians. BUCKLEY *et al.* (2000) included *Notosuchus* in the same clade along with *Libycosuchus* and a subgroup composed by *Uruguaysuchus*, *Simosuchus* and *Malawisuchus*. In a much broader framework (POL, 1999, 2003; POL & NORELL 2004a, 2004b; POL & APESTEGUIA, 2005), *Notosuchus* is considered a sister-group to a branch composed by *Comahuesuchus*, *Baurusuchus*, *Bretesuchus*, *Iberosuchus*, *Chimaerasuchus* and *Sphagesaurus*. ZAHER *et al.* (2006) further add *Mariliasuchus* to this list.

Although it is difficult to extract a common sense upon the mixture of results presented by these various frameworks, in a broader view most works agree that *Notosuchus* relates closely to Comahuesuchidae, Sphagesauridae, Baurusuchidae and Bretesuchidae (POL, 1999, 2003; ORTEGA *et al.*, 2000; MARTINELLI, 2003; POL & NORELL 2004a, 2004b; POL & APESTEGUIA, 2005; ZAHER *et al.*, 2006). Main problems and alternative relationships obtained may be regarded, for most cases, as the result of differential absence of certain taxa from each analysis.

THE BRAZILIAN NOTOSUCHID FROM MARÍLIA

Mariliasuchus amarali Carvalho & Bertini, 1999 is another South American species, described from the Upper Cretaceous of the Bauru Group, Brazil (Fig.2). *Mariliasuchus* was extensively described by CARVALHO & BERTINI (1999), ANDRADE (2005), VASCONCELLOS & CARVALHO (2005, 2006), ANDRADE *et al.* (2006) and ZAHER *et al.* (2006), all focusing on cranial features and most also addressing its relationships with other notosuchians.

Most descriptive details published can be seen in Zaher *et al.* (2006), but also in Andrade *et al.* (2006) for specific focus on the choanae. Vasconcellos & Carvalho (2005, 2006) studied the ontogeny of *Mariliasuchus* and other works (Carvalho *et al.*, 2004; Fiorelli, 2005) included the species in broad phylogenetic analysis of crocodylomorphs.

Mariliasuchus is well represented in Brazilian paleontological collections (UFRJ-DG, IGCE-UNESP/ Rio Claro, MN-UFRJ, and MUZUSP). As for *Notosuchus*, the large number of specimens contributes to the knowledge of this taxon. Nevertheless, until most recently the holotype was the only specimen with a published description (Carvalho & Bertini, 1999). The holotype is truly a juvenile, which can be inferred by its small size, proportionally large orbits (Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006) and the unfused interfrontal suture (as in Carvalho & Bertini, 1999; p.93, fig.7). A few new specimens (UFRJ-DG-56-R, UFRJ-DG-105-R, UFRJ-DG-106-R) were reported by Vasconcellos & Carvalho (2005, 2006) and others (MN 6298-V, MN 6756-V, MZSP-PV-50, MZSP-PV-51) were addressed by Zaher *et al.* (2006). MN 6756-V is figured in Azevedo *et al.* (2004). As previously mentioned by Zaher *et al.* (2006), the MN specimens have an intermediate size between the holotype and the MUZUSP specimens and also possibly constitute semi-adult individuals. In an unpublished work, Andrade (2005) introduced three specimens that can be considered as semi-adults, which are briefly presented here.

Mariliasuchus was initially identified as a Notosuchidae through anatomical comparison (Carvalho & Bertini, 1999). The first phylogenetic analysis including the species (Carvalho *et al.*, 2004) proposed a closer relationship with *Candidodon itapecuruense* Carvalho & Campos, 1988, from the São Luis-Grajaú Basin (Itapecuru Group, Lower Cretaceous; Rossetti, 2001). Andrade (2005), Fiorelli (2005) and Marconato (2006), in unpublished works, also included *Mariliasuchus* in a phylogenetic analysis, obtaining a closer relationship with *Notosuchus*. Phylogenetic hypothesis by Zaher *et al.* (2006) presented *Mariliasuchus* as the sister-group of *Comahuesuchus brachybuccalis* Bonaparte, 1991, from the Neuquén Basin (Bajo de la Carpa Formation, Upper Cretaceous; Leanza *et al.*, 2004), Argentina.

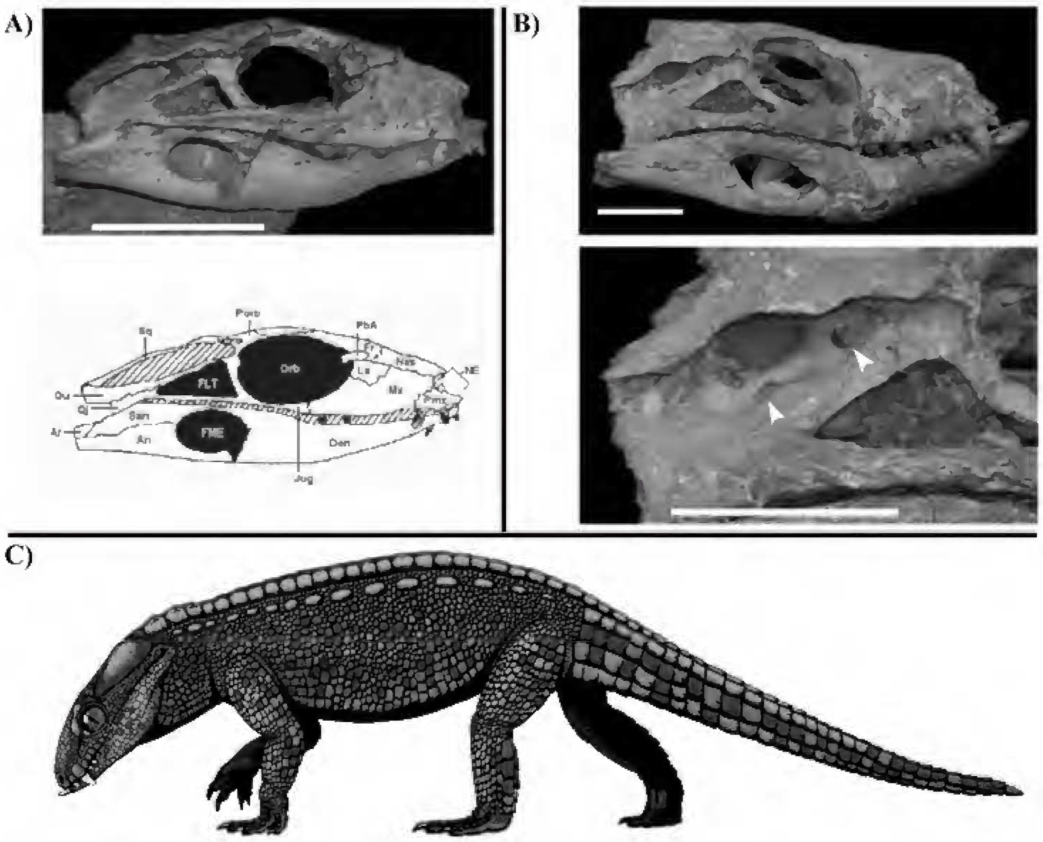

Fig.2- Main aspects of *Mariliasuchus amarali*: A) UFRJ-DG-50-R, holotype, a juvenile specimen; B) mature specimen UFRJ-DG-106-R, showing a detail of the quadrate surface; C) paleoartistic reconstruction of *Mariliasuchus*. Note white pointers, showing quadrate fenestrae. Bar = 20mm. (UFRJ-DG-50-R drawing adapted from Carvalho & Bertini, 1999; C - by Felipe Alves Elias).

Carvalho *et al.* (2004) chose to include *Mariliasuchus* in the then defined phylotaxon Candidodontidae. Nevertheless, *Candidodon* lacks several morphological characteristics of *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006). The general set of characteristics seems to indicate that *Candidodon* may be more similar to Uruguaysuchidae (*sensu* Gasparini, 1971), although with a single naris (Nobre & Carvalho, 2002). The lack of morphological information on the skull of *Candidodon* clearly introduces a problem, especially regarding the relationship of palatine and choanal elements, as stated by Andrade *et al.* (2006). The phylogenetic relationships obtained in posterior studies indicate that *Mariliasuchus*, *Notosuchus*, *Comahuesuchus* and possibly *Sphagesaurus* are closely related (Andrade, 2005; Fiorelli, 2005; Zaher *et al.*, 2006).

The recently published phylogenetic study by Zaher *et al.* (2006) shows *Mariliasuchus* as sister-group to *Comahuesuchus*, an exclusive relationship supported by several characters (*e.g.*, jugal foramen present, maxilla reaching the orbit, anterior procumbent alveoli). The relevance of these characters and their occurrences in other taxa is still open to debate, as suggested by other works (Martinelli, 2003; Andrade, 2005).

Geological Settings

Both *Notosuchus* and *Mariliasuchus* have a reasonably common geological provenance. They are Upper Cretaceous notosuchians that inhabited different areas of Central to Southern South-America. Although these areas were distant, they represent cratonic structures rather than marine sediments. In both cases, the sedimentary units are interpreted as semi-arid environments, suggesting a similar ecologic background. While the geological settings for *Notosuchus* are fairly known, there is some disagreement on *Mariliasuchus* specific settings.

Notosuchus terrestris specimens come from an extensive area in Patagonia (Fig.3), from at least two localities (Neuquén and Rio Negro provinces), housed by many institutions (MACN, MLP, MPCA, MUCPv-UNC). *Notosuchus* is found in deposits of the Bajo de La Carpa Formation, which is part of the Rio Colorado Subgroup and the Neuquén Group, Neuquén Basin (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991; Leanza *et al.*, 2004). The age of the Bajo de la Carpa Formation is most probably Santonian (Leanza *et al.*, 2004). These sediments are usually composed of fine to coarse grained reddish to whitish sandstones,

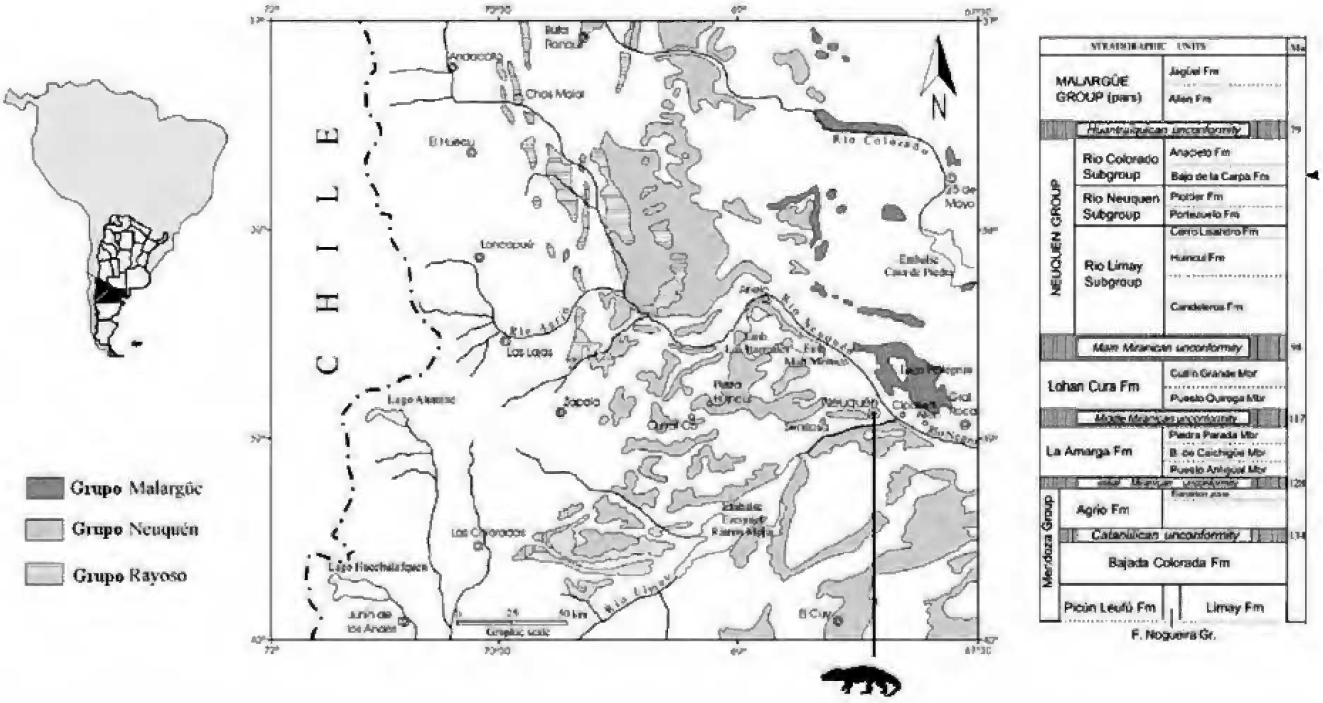

Fig.3- Geographical distribution and stratigraphical range of *Notosuchus terrestris*. The stratigraphical diagram (right) shows the Cretaceous geological units of the Neuquén Basin in the Neuquén Province, and the position of the Bajo de La Carpa Formation (modified from Leanza *et al.*, 2004).

with carbonatic nodules and mudstone lenses (Leanza *et al.*, 2004; Andrade, 2005; Candeiro & Martinelli, 2006).

Mariliasuchus amarali comes from the Upper Cretaceous of Bauru Group (*sensu* Batezelli *et al.*, 2003), Southwestern Brazil (Fig.4). The specific geological settings for this species have become controversial, mostly because a new terminology has been adopted for the Bauru Group sediments. All specimens come from the vicinities of Marília City (São Paulo State, Brazil) (Carvalho & Bertini, 1999, 2000; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006), collected from at least four sites (Nava, 2004). The holotype and the URC specimens come from Rio do Peixe outcrop, close to the Peixe River (Carvalho & Bertini, 1999, 2000; Andrade, 2005). Most authors refer to the sediments as the lower layers of the Adamantina Formation (Carvalho & Bertini 1999, 2000; Kellner & Campos, 1999; Dias-Brito *et al.*, 2001; Vasconcellos & Carvalho, 2005; Candeiro *et al.* 2006) but these have been recently recognized as a distinct formation. The lower Adamantina layers, where there is a predominance of siltic matrix over sandstone, are now considered a part of the Araçatuba Formation (Batezelli, 1998, 2003; Batezelli *et al.*, 1999, 2003; Fernandes *et al.*, 2003; Nobre & Carvalho, 2006). Vasconcellos & Carvalho (2006) not only recognize the current model, but also consider the difficulties in the determination of the limits between units. These authors identified the provenance of the specimens as near the contact between the Araçatuba and Adamantina formations. Zaher *et al.* (2006) also recognize the occurrence of the Araçatuba Formation at Rio do Peixe area, but identify the provenance of the fossil material as the upper levels of the Adamantina Formation, closer to the contact with the Marília Formation.

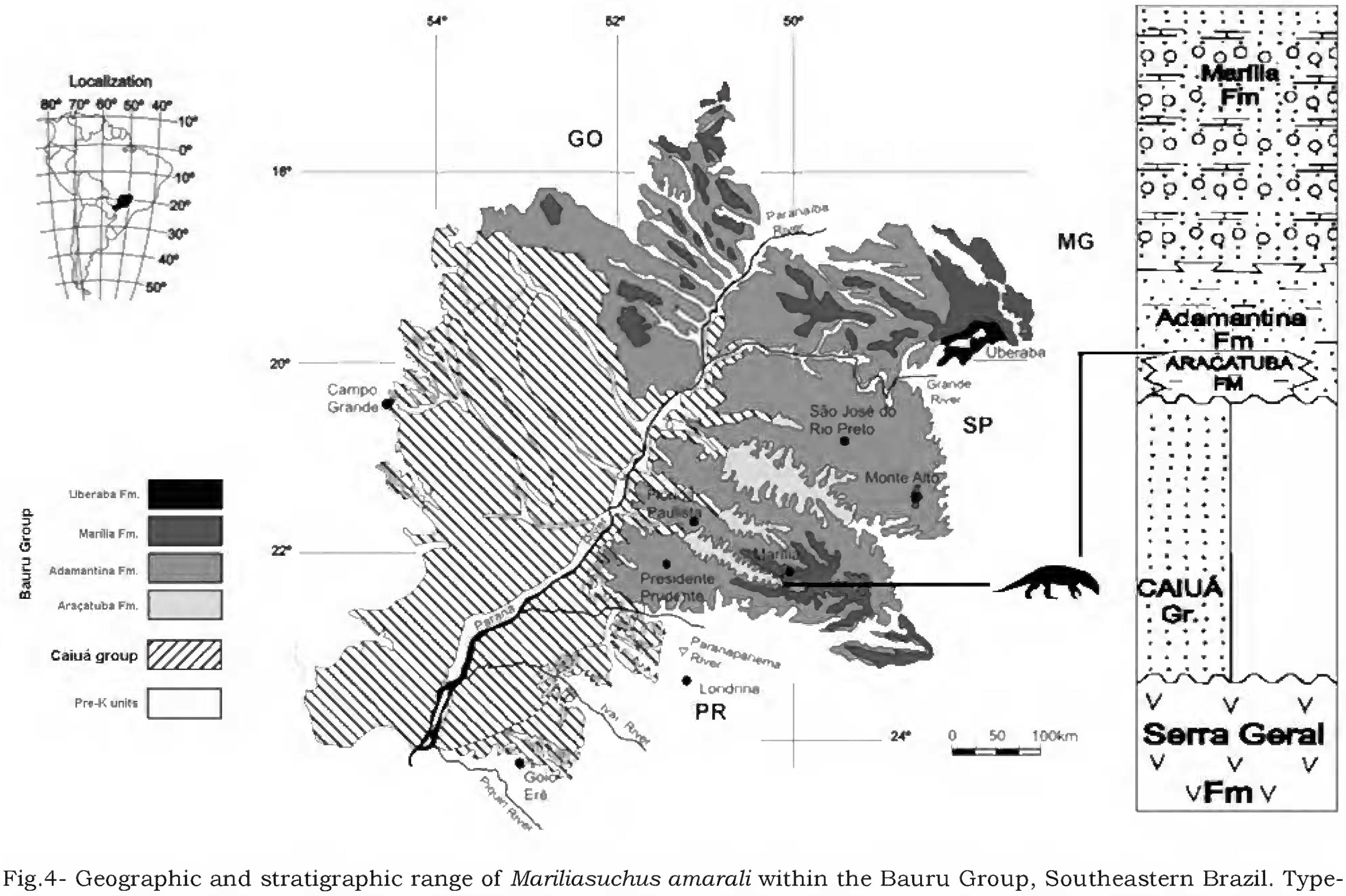

Fig.4- Geographic and stratigraphic range of *Mariliasuchus amarali* within the Bauru Group, Southeastern Brazil. Type-locality indicated, at the vicinities of Marília. The lithological column (right) shows the distribution of the Cretaceous geological units in the State of São Paulo, and the relative position of the Araçatuba Formation. Note that the Bauru Group extends over a large area, including the states of Goiás (GO), Minas Gerais (MG), Paraná (PR) and São Paulo (SP). (Map compiled from Fernandes & Coimbra, 1996; Batezelli, 1998; lithological column modified from Batezelli, 2003).

Actually, as the Araçatuba and Adamantina formations interbed, and were probably synchronic, it is possible that *Mariliasuchus* remains may eventually be recovered from both the Araçatuba and the Adamantina formations. This idea is supported by Nava's (2004) statement that specimens were not found in a single site. However, the occurrence of *Mariliasuchus* in the upper levels of the Adamantina Formation is yet to be properly reported, especially including material from other outcrops.

The sediments of the Araçatuba Formation are usually composed of greenish to brownish mudstones, interbedded with fine-grained sandstone lenses. *Mariliasuchus* material usually comes from such lenses and, as in the case of URC•67, can be associated with carbonatic nodules. The Araçatuba Formation may be positioned over deposits of either the Caiuá Group (probably middle Cretaceous) or the older basaltic Serra Geral Formation (Lower Cretaceous), depending on the area of occurrence. It is always overlaid by the sediments of the Adamantina Formation (Bauru Group), and although its extension is not small, only a minor part is exposed on the surface (Paula e Silva *et al.*, 2003).

Further debate also exists on the age of the Upper Cretaceous deposits from the Bauru Group. Dias-Brito *et al.* (2001) argue for a Turonian-Maastrichtian age for the Bauru Group, with a Campanian depositional hiatus, indicating an early age for the Araçatuba Formation sediments, possibly Turonian. The proposal by Dias-Brito *et al.* (2001) is widely adopted (Vasconcellos & Carvalho, 2005, 2006; Nobre & Carvalho, 2006; Zaher *et al.*, 2006). Nevertheless, the existence of several gradational contacts between the Adamantina and Marília formations is widely recognized (Batezelli, 1998, 2003; Batezelli *et al.*, 1999, 2003; Zaher *et al.*, 2006), which implies that a Campanian depositional hiatus is unlikely to occur.

Correlations based on charophytes, ostracods and vertebrates (Gobbo-Rodrigues *et al.*, 2000a, 2000b, 2000c; Gobbo-Rodrigues, 2001; Santucci & Bertini, 2001) indicate that the Araçatuba Formation was most probably Campanian (Fig.4), rather than Turonian. Although the age attributed for *Mariliasuchus* is similar for Zaher *et al.* (2006) (Campanian-Maastrichtian), it should be noticed that both models represent different interpretations of the data available. Zaher *et al.* (2006) follows the basic correlation model proposed by Dias-Brito *et al.* (2001) without the Campanian hiatus, and considers that *Mariliasuchus* comes from the upper Adamantina layers. We consider that *Mariliasuchus* comes from the Araçatuba Formation, and follow the Gobbo-Rodrigues (2001) model for age correlation.

Other notosuchians possibly related with either *Notosuchus* or *Mariliasuchus* come from a similar broad geological background. *Candidodon itapecuruense* was found in deposits of the São Luis-Grajaú Basin (Brazil), previously included in the Parnaiba Basin (Rossetti, 2001). The structure of its sedimentary units is under revision. *Candidodon* was previously referred to as from the Itapecuru Formation, but this unit was redescribed as a Group and divided into other units (Rossetti, 2001). The specimens probably come from the lower layers of the Itapecuru Group, currently referred to 'undifferentiated unit' by Rossetti (2001). Palinologic data from correlated localities (Guariba and Querru outcrops) suggest a meso-Albian age (Lower Cretaceous) for *Candidodon* (Pedrão *et al.*, 1993; Carvalho & Bertini, 2000). *Comahuesuchus brachybuccalis* was found in the Bajo de la Carpa Formation (Neuquén Basin, Upper Cretaceous, Argentina). Considering the geological settings, *Comahuesuchus* and *Sphagesaurus* are notosuchians that share the stratigraphic range of both *Notosuchus* and *Mariliasuchus*. *Comahuesuchus* also shares the same geographical provenance of *Notosuchus*, while *Sphagesaurus* share a similar geographical provenance with *Mariliasuchus*.

ABBREVIATIONS

Institutional. IGCE-UNESP, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Rio Claro, Brazil; MACN, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MLP, Museo de La Plata, La Plata, Argentina; MN-UFRJ, Museu Nacional, UFRJ, Rio de Janeiro, Brazil; MPCA, Museo "Carlos Ameghino", Cipoletti, Argentina; MUCPv, Museo de la UNC, Neuquén, Argentina; MUZUSP, MZSP, Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil; UFRJ, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Brazil; UFRJ-DG, Departamento de Geologia, UFRJ, Rio de Janeiro, Brazil; UNC, Universidad Nacional del Comahue, Neuquén, Argentina; URC, Museu "Paulo Milton Barbosa Landim", IGCE-UNESP, Rio Claro, Brazil.

Anatomical. An, angular; Ar, articular; Boc, basioccipital; Bes, basiesphenoid; BPO, postorbital bar; c, caniniform; Den, dentary; Eoc, exoccipital; Ept, ectopterygoid; FAO, antorbital fenestra; FLT, laterotemporal fenestra; FME, external mandibular fenestra; FMP, maxilo-palatine fenestra; FPMM, premaxilla-maxilla foramen; Fr, frontal; FSO, suborbital fenestra; FST, supratemporal fenestra; i, incisiform; Jug, jugal; La, lachrymal; m, molariform; Mx, maxilla; Na, nasal; NE, external naris; NI, internal naris (choana); Orb, orbit; Pal, palatine; Par, parietal; PbA, palpebral (anterior); Pfr, prefrontal; pm, premolariform; Pmx, premaxilla; Porb, postorbital; PRA, retroarticular process; Pt, pterygoid; Qj, quadrate-jugal; Qu, quadrate; San, surangular; SIC, interchoanal septum; Sp, splenial; Sq, squamosal; Sy, symphysis.

MATERIAL, PRESERVATION, AND VARIABILITY

Studied material

A small number of specimens of *Mariliasuchus amarali* (URC R•67, URC R•68, URC R•69) was studied in the IGCE-UNESP Collection (Rio Claro *Campus*, Brazil), but also from MN-UFRJ (Rio de Janeiro, Brazil). The specimens were composed mostly by cranial material, although URC R•67 also has well preserved cervical vertebrae and ribs. In contrast, a representative number of specimens from *Notosuchus terrestris*, comprising no less than 45 individuals, was studied from the collections of MACN, MLP and MPCA, all from Argentina. Most specimens included only cranial material, although MACN-Pv-RN-1037 also preserves postcranial elements. Furthermore, other species were observed, including most of the existing specimens of *Comahuesuchus*. A complete list of specimens of notosuchians included in this study can be seen in Appendix 1.

Preservation

Most specimens of *Notosuchus* and *Mariliasuchus* show some degree of deformation and thus a few aspects of the morphology could not be taken from a single specimen. This can be related to differences observed in both notosuchians and must not be confounded with intraspecific variability. The material from both species may be broken, incomplete, deformed, showing eroded surfaces and delicate structures are missing. However, it was possible to recognize that specimens of *Mariliasuchus* are usually better preserved than those of *Notosuchus*. Particularly in *Notosuchus*, no single specimen has shown a really good preservation throughout the entire skull, considering the studied material. Examples of structures clearly identified in *Mariliasuchus*, but not easily seen in *Notosuchus* due to preservation problems, are the medial borders of the maxillo-palatine fenestrae, the interchoanal septum and teeth ornamentation. Furthermore, a greater number of *Mariliasuchus* specimens include associated (or even articulated) postcranial remains.

Most specimens of *Notosuchus* include at least some degree of deformation (MACN-Pv-RN-1041, MACN-Pv-RN-1046, MACN-Pv-RN-1048, MACN-Pv-RN-1118, MACN-Pv-RN-1119, MPCA-Pv-789, MPCA-Pv-791) and two (MACN-RN-1037, MACN-Pv-RN-1041) have a broken rostrum (thrusted downwards). The lectotype, MLP 64-IV-16-5, has an abnormally enlarged antorbital fenestra due to preservation problems (Fig.1B) and most of the skull surface suffered from either abrasion or corrosion, lacking most of the original ornamentation. Although the right fenestra is altered, the left antorbital fenestra is smaller, with a different morphology and smooth borders, as in MACN-Pv-N-24 (see Bonaparte, 1991). This specific problem was previously addressed by Woodward (1896) himself. On the other hand, the most complete specimen regarding presence of elements is MACN-Pv-RN-1037, which includes most of the skull and mandibles, cervical and dorsal vertebra and anterior appendicular remains, these described by Pol (2005). Other two specimens (MACN-Pv-RN-1041, MACN-Pv-RN-1045) include skulls that can be considered as reasonably preserved. Several partial specimens, despite damaged, are especially valuable (MACN-Pv-N-22, MACN-Pv-N-23, MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-11, MLP-64-IV-16-13, MLP-64-IV-16-14, MLP-64-IV-16-15, MLP-64-IV-16-16, MLP-64-IV-16-23, MLP-64-IV-16-24). Though partial remains, these specimens provide a lot of quality information as some of them are beautifully preserved, showing sutures and details that are often not evident in more complete specimens, as previously pointed out by Andrade *et al.* (2006) for *Sphagesaurus* and *Stratiotosuchus*.

Although the *Mariliasuchus* material shows good preservation, specimens are not free from problems. URC R•67 is a most complete set of skull and mandible, including cervical vertebrae and ribs, with the skull showing dorsoventral deformation. URC R•68 is a partial rostrum and mandible, including the right side of the rostrum and dental series, as well as most of the right hemimandible and the symphyseal part of the left hemimandible, showing no identifiable deformation. Though the specimen is broken and constitutes only a part of a skull, each element shows an exquisite preservation. URC R•69 includes only the occipital surface and the left quadrate, but most other elements were destroyed. MN 6298-V lacks the mandible and does not preserve the left posterior elements of the skull. MN 6756-V is mostly complete, with a well preserved set of skull and mandible. In Zaher *et al.* (2006; p.7, 2nd column, lines 8-15), the identification of MN specimens is changed, as MN 6298-V is identified as MN 6756-V and vice versa (as also in Azevedo *et al.*, 2004).

Lateral compression can be identified in the MN specimens and UFRJ-DG-105-R, due to the deformation of the suborbital fenestrae. Although UFRJ-DG-105-R and UFRJ-DG-106-R are partial skulls, they are well preserved and include the mandible. UFR-DG-56-R is poorly preserved and was subject to severe deformation. MUZUSP specimens may be the most complete and better preserved, as described by Zaher *et al.* (2006), although MZSP-PV-50 shows a reasonable amount of damage on the dorsal surface of the rostrum (Zaher *et al.*, 2006; p.9; Fig.5). UFRJ-DG-56-R and URC R•69 are badly damaged skulls (Vasconcellos & Carvalho, 2006; Andrade, 2005) and information on these specimens should be considered with caution.

Variation among specimens and true intraspecific variability

Differences in the morphology are the basis for the erection of new fossil species. However, morphological evidence for a new taxon should be constant and allow the recognition of each species, provided the relevant structures are preserved. Differences in the morphology are often regarded as evidence of new species, but not all structures show a constant morphology and, thus, can be regarded as suitable evidence supporting the recognition of different species. Intraspecific variability constitutes a simpler explanation and very common source of morphological differences among individuals in extant taxa. Furthermore, preservation may be an important factor to be considered regarding fossil groups (Holz & Schultz, 1998; Holz & Souto-Ribeiro, 2000; Holz & Simões, 2002). In fossil taxa the reduced sample of specimens is often a problem, as continuous variable characters may appear to be distinct discrete states and discrete states of a character may not be represented in the sample.

Notosuchus and *Mariliasuchus* constitute exceptions in the study of fossils, as the elevated number of specimens contributes to the identification of minor population differences, which may occur within one species or the other. For *Notosuchus*, both Andrade (2005) and Fiorelli (2005) identified variability on the morphology of the parietal, which was considered as related to sexual dimorphism. In *Mariliasuchus*, Zaher *et al.* (2006) identified variability in the development of ornamentation, presence (or absence) frontal medial ridge, parietal width between the supratemporal fenestra and teeth implantation.

Regarding *Mariliasuchus*, the occurrence of ornamentation and frontal ridge may be easily misinterpreted due to preservation. The presence of ornamentation, even if regarded to be of biological origin, may also interfere with the development of the frontal ridge. It is thus preferable not to consider a particular hypothesis to explain this variability, while a broader range of specimens awaits description. In *Notosuchus*, differences are often the result of poor preservation. Good examples include: (i) the description of *Notosuchus lepidus*, based in damaged and partially reconstructed specimens (Gasparini, 1971); (ii) the reinterpretation of the palatine-ectopterygoid contact by Martinelli (2003), which the suture is positioned in the palatine bar, medially to the taphonomic features previously regarded as the suture. In both cases, characters involved are not truly variable. Instead, the poor preservation prevented the correct identification of the morphology. In *Notosuchus*, further disagreement between previous published studies affects several aspects of the morphology, such as the orientation of the retroarticular process, general profile of the mandible, elongation of the symphysis, presence of teeth ornamentation and interchoanal septum (Fig.1).

True variability

Despite problems of preservation, true variability can be identified in *Notosuchus* and *Mariliasuchus*, whenever selected specimens are taken. In *Notosuchus*, true variability mostly relates to the parietal morphology, which is discussed below. In *Mariliasuchus*, this applies at least to parietal width and teeth implantation.

Zaher *et al.* (2006) suggested that the *Mariliasuchus* specimen with wider parietals (MZSP-PV-51) may constitute a different species, but preferred to assume either sexual dimorphism or individual variation to explain differences. Teeth implantation is also variable, as maxillary and mandibulary teeth may be oblique or not oblique (Zaher *et al.*, 2006). As in *Notosuchus* and *Sphagesaurus*, oblique implantation only affects middle and posterior teeth and is always present as a paramesial rotation of the crown. The good preservation of specimens indicates that they are unlikely to reflect taphonomic bias and there is no evidence suggesting an ontogenetic trend toward obliquely implanted teeth. Thus, populational variation is currently the simplest explanation. Other aspects of the variability in *Mariliasuchus* have been explained as the result of ontogenetic changes (Vasconcellos & Carvalho, 2005, 2006), as discussed below.

It should be noticed that, currently, no particular difference could be linked to any other variable character, layer or site of collection, either in *Mariliasuchus* or *Notosuchus*. This indicates there seems to be no particular population in space and time sharing a set of characters that could justify the identification of distinct populations. Variability has been explained as the result of other biological aspects of these species (ontogeny, sexual dimorphism, individual differences within the population) or even preservation (Andrade, 2005; Fiorelli, 2005; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). Furthermore, the common paleogeographic and stratigraphic provenance of specimens does not support the existence of new species within each genera.

Ontogenesis and developmental stages of the specimens

An important aspect already recognized on the intraspecific variability refers to ontogenesis. Most specimens of *Notosuchus* are adults (Andrade, 2005), with a small proportion of young (MLP-64-IV-16-24) and sub-adult (MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-8) individuals among the specimens studied (±8.5%). In *Mariliasuchus* this proportion is more expressive (±50%), considering the total specimens officially reported. The most relevant specimen on ontogenetic studies may be the holotype UFRJ-DG-50-R, which is currently the smallest specimen, widely recognized as the youngest individual (Carvalho & Bertini, 1999; Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006). The URC and the MN specimens show an intermediate size, bigger than the holotype and smaller than MZSP-PV-50. Among them, MN 6756-V is the smallest and URC R•68 is the largest specimen (Tab.1). Recognition of this difference between the *Mariliasuchus* and *Notosuchus* samples is important, because the ontogeny can be a source of morphological variability, especially in the sample of *Mariliasuchus*. The same argument can barely apply for the studied specimens of *Notosuchus*, as only a low percentage of them are not adult specimens.

Vasconcellos & Carvalho (2005, 2006) demonstrated that significant changes occur during the development of *Mariliasuchus*. These includes the caudal displacement of the mandibular and laterotemporal fenestrae, as well as an increment of size of the supratemporal and laterotemporal fenestra, with implications in the proportional volume of muscles associated with these fenestrae. Nonetheless, the study does not clarify most changes affecting characters used in phylogenetic studies. Furthermore, although ontogenetic changes are reasonably described for *Mariliasuchus*, they are virtually unknown for *Notosuchus*. The description of young specimens may be particularly important to allow comparison and improve understanding on the evolution and development of notosuchians.

Problems of interpretation of the dental formula

Both in *Notosuchus* and *Mariliasuchus*, an important problem affecting the comprehension of variability regards the interpretation of the dental formula. In *Mariliasuchus*, the original description (Carvalho & Bertini, 1999) accounted for three premaxillary teeth, at least three maxillary teeth and at least two mandibulary teeth. Of these, the third (and last) premaxillary tooth was a hypertrophied caniniform. Although this constitutes poor information, teeth were simply not accessible in the specimen, which was preserved with jaws in occlusion and attempts to free the mandible would have inflicted damage to the material. The unpublished work of Andrade (2005) further extends the information on the dental formula, confirming three teeth on the premaxilla, the third one been the hypertrophied caniniform, six maxillary and nine mandibulary teeth. Zaher *et al.* (2006) provide an alternative interpretation for the dental formula, with four premaxillary (the last one been the first postcaniniform) and five maxillary teeth. All works agree with nine teeth in the mandible.

Dentition is difficult to access in *Notosuchus*, as the overall preservation is poor and most specimens with reasonably complete skulls have the mandible in occlusion, preventing access to the teeth. Nevertheless, the oblique implantation was only well represented by Woodward (1896; Plate II) and is beautifully exposed in several MLP partial specimens (MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-13, MLP-64-IV-16-16, MLP-64-IV-16-23). Woodward (1896; as Gasparini; 1971; Bonaparte, 1991) originally considered two small cylindrical teeth (incisiforms) in the premaxilla, and a possible third small tooth preceding them, below the naris. The presence of this anteriormost tooth is confirmed in MACN-Pv-RN-1038 and MACN-Pv-RN-1040, while the same area is not reasonably preserved in other specimens. These incisiforms were followed by a well developed caniniform tooth, robust and long-rooted (Woodward, 1896; Gasparini, 1971; Bonaparte, 1991), also in the premaxilla. The first postcaniniform tooth from the upper series was considered by Woodward (1896) and Gasparini (1971) as pertaining to the maxilla. Bonaparte (1991; p.36, 2nd§) describes the first post-caniniform as of difficult identification, as in lateral view it seemed to be related to the maxilla, and in palatal view it could be related to the premaxilla. Eventually, Bonaparte (1991; p.43, 1st§) refers to it for the first time as part of the premaxillary series, although representing it as a maxillary tooth (Bonaparte, 1991; fig.3, p.33; fig.5, p.37). The following teeth would comprise six elements, according to Woodward (1896) and Gasparini (1971), but Bonaparte (1991) suggested their number could reach up to 10 teeth. The number of mandibulary elements is probably 10 (Woodward, 1896; Gasparini, 1991) despite problems of preservation, which suggest a similar number for the complete upper series.

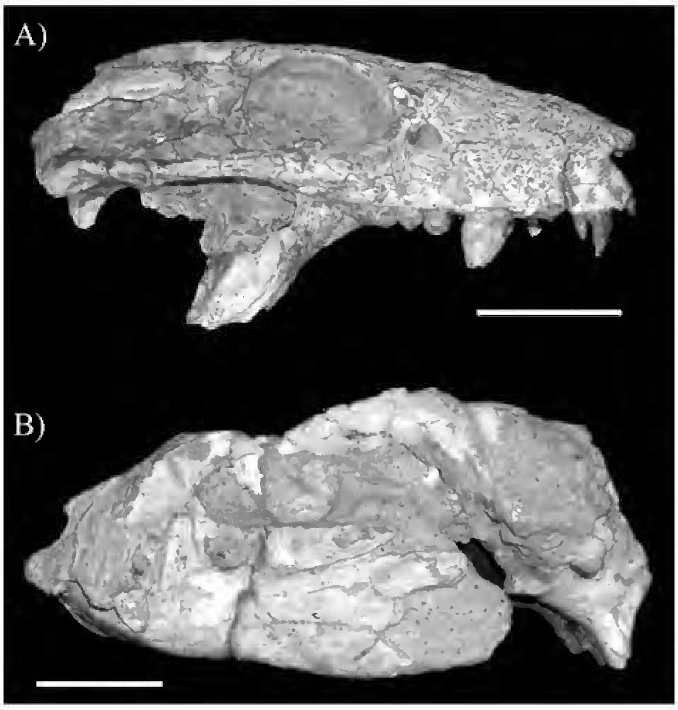

Fig.5- Cranial material from other species of notosuchians, which have been related to *Mariliasuchus* by previous cladistic analysis. A) right side of the skull of *Candidodon itapecuruense* UFRJ-DG-114-R, a referred specimen; B) left side of the skull of *Comahuesuchus brachybuccalis* MUCPv-202, holotype. Bar = 20mm.

TABLE 1. Summary of *Notosuchus* and *Mariliasuchus* specimens considered in this study, showing general state of the material and completeness.

Feature	*Notosuchus* specimens	*Mariliasuchus* specimens
Specimens including cranium and postcranium	MACN-Pv-RN-1037, MPCA-Pv-789	MN 6756-V, MZSP-PV-50, MZSP-PV-51, **UFRJ-DG-50-R**, UFRJ-DG-106-R, URC R•67
Non-adult specimens	MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-8, MLP-64-IV-16-24	MN 6298-V, MN 6756-V, **UFRJ-DG-50-R**, URC R•67, URC R•68, URC R•69
Badly crushed skulls	MACN-Pv-RN-1046, MACN-Pv-RN-1048	UFRJ-DG-56-R
Partial skulls, including rostrum or rostrum and symphysis preserved	MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MLP-64-IV-16-6, MLP-64-IV-16-11, MLP-64-IV-16-15, MLP-64-IV-16-16, MLP-64-IV-16-23, MLP-64-IV-16-24	URC R•68
Partial skulls, including rostrum, orbits and skull table	MACN-Pv-N-23, MACN-Pv-N-107, MACN-Pv-RN-1046, MACN-Pv-RN-1048, MACN-Pv-RN-1118, MACN-Pv-RN-1119, MLP-64-IV-16-1, MLP-64-IV-16-2, MLP-64-IV-16-7, MLP-64-IV-16-8, MLP-64-IV-16-31, MPCA-Pv-789/1, MPCA-Pv-791	UFRJ-DG-56-R
Skulls mostly preserved	MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045, MLP-64-IV-16-3, **MLP-64-IV-16-5**	MN 6298-V, MN 6756-V, MZSP-PV-50, MZSP-PV-51, UFRJ-DG-50-R, UFRJ-DG-105-R, UFRJ-DG-106-R, URC R•67
Sample	46 (45 studied)	13 (8 studied)

Type specimens in bold.

As seen above, there is disagreement on the interpretation of distribution of dental elements in the premaxilla and maxilla of both *Mariliasuchus* and *Notosuchus*. Here, the first postcaniniform is considered as originally pertaining to the maxillary series, following the traditional descriptions of *Mariliasuchus* (CARVALHO & BERTINI, 1999) and *Notosuchus* (WOODWARD, 1896; GASPARINI, 1971), but also based on the studied specimens, as described below.

MORPHOLOGICAL COMPARISON OF *MARILIASUCHUS* AND *NOTOSUCHUS*

Mariliasuchus amarali and *Notosuchus terrestris* were considered similar species by CARVALHO & BERTINI (1999), who present a general comparison with several other mesoeucrocodylians. This comparative analysis focuses on the morphology of both species, along with *Candidodon itapecuruense* Carvalho & Campos, 1988 and *Comahuesuchus brachybuccalis* Bonaparte, 1991. *Candidodon* and *Comahuesuchus* were considered respectively by CARVALHO *et al.* (2004) and ZAHER *et al.* (2006) the sister group of *Mariliasuchus*. Though most of these species are extensively described in the bibliography, it should be noticed that information on the skull of *Candidodon* is limited (CARVALHO, 1994; NOBRE & CARVALHO, 2002), lacking detailed interpretation of sutures.

ROSTRUM AND GENERAL FEATURES OF THE SKULL – The general proportions of the skull are similar (Fig.6), with rostrum length as short as the postorbital region. The general shape of the skull is mostly similar for *Notosuchus* and *Mariliasuchus*, where the rostrum is small but clearly distinguishable from the rest of the skull. This can better be seen in adult specimens. In *Notosuchus*, the limits of the rostrum are not so evident in younger specimens (MACN-Pv-N-43, MLP-64-IV-16-7, MLP-64-IV-16-24), and the same happens in the case of *Mariliasuchus* holotype. Subadult specimens of *Mariliasuchus* (URC R•67, MN 6298-V, MN 6756-V) show evident rostrum limits, but less evident than in MZSP specimens, which are adults. Both in *Notosuchus* and *Mariliasuchus*, the source of variability is most likely ontogenetic (see VASCONCELLOS & CARVALHO, 2005, 2006, for *Mariliasuchus* ontogenetic development). Neither *Candidodon* nor *Comahuesuchus* show similar characteristics, though the rostrum of the last is extremely short (BONAPARTE, 1991). In both cases, the rostrum fits gradually to the skull. In the different specimens of *Comahuesuchus*, there seems to be no particular straightening of the rostrum, and MOZ-P-6131 (the biggest specimen; MARTINELLI, 2003) show a wide rostrum, as the other smaller specimens.

Mariliasuchus and *Notosuchus* have the same type of ornamentation (Fig.7), characterized by irregular sulcation. This ornamentation develops on the skull, although mainly over the rostrum. This type of ornamentation is not exclusive to them and can be found also in baurusuchids and *Comahuesuchus*, among others. Ornamentation composed by subpolygonal pits, on the other hand, is usually seen in neosuchians, peirosaurids and *Araripesuchus* (BENTON & CLARK, 1988; CLARK, 1994; ORTEGA *et al.*, 2000), but also in *Candidodon*.

In *Notosuchus, Mariliasuchus, Comahuesuchus* and *Candidodon* the nares are single and terminal. Though in *Comahuesuchus* they were considered as 'inset' (SERENO *et al.*, 2003), this was related to a preservation problem on the specimens described by BONAPARTE (1991). Description of MOZ-P-6131 shows that *Comahuesuchus* have a truly terminal naris (MARTINELLI, 2003). Nasals have a similar general profile in *Notosuchus, Mariliasuchus* and *Comahuesuchus*, but not in *Candidodon*. In the first three notosuchians, the nasals contribute anteriorly to the naris and widen posteriorly near the contact with the lachrymals, straightening again at the contact with the frontal. In dorsal view, this triangular to rhomboidal profile is common to *Sphagesaurus*, but is apparently absent from *Candidodon* (ANDRADE, 2005). Other mesoeucrocodylians usually have straight nasals, with paralleled lateral borders, including *Araripesuchus, Anatosuchus* and most neosuchians. Thalattosuchians constitute an exception, as they also have triangular nasals (ANDREWS, 1913).

Further similarities can be seen between *Notosuchus, Mariliasuchus* and *Comahuesuchus*. As in BONAPARTE (1991), *Notosuchus* shows a small anterior projection of the nasals over the naris (Fig.6). The structure is preserved in several specimens (MACN-Pv-N-24, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1040, MACN-Pv-RN-1041, MACN-Pv-RN-1119, MLP-64-IV-16-1, MLP-64-IV-16-5, MLP-64-IV-16-6, MLP-64-IV-16-22, MPCA-Pv-791). The projection itself has a triangular outline, extending slightly over the naris, but not exceeding the mesial border of the premaxilla. VASCONCELLOS & CARVALHO (2005) have already pointed out the possible presence of a small anterior projection of the nasals in *Mariliasuchus*, without the development of an internarial bar. The structure was considered present in UFRJ-DG-105-R and also probably in the holotype. ZAHER *et al.* (2006) ignored the occurrence of the structure, but

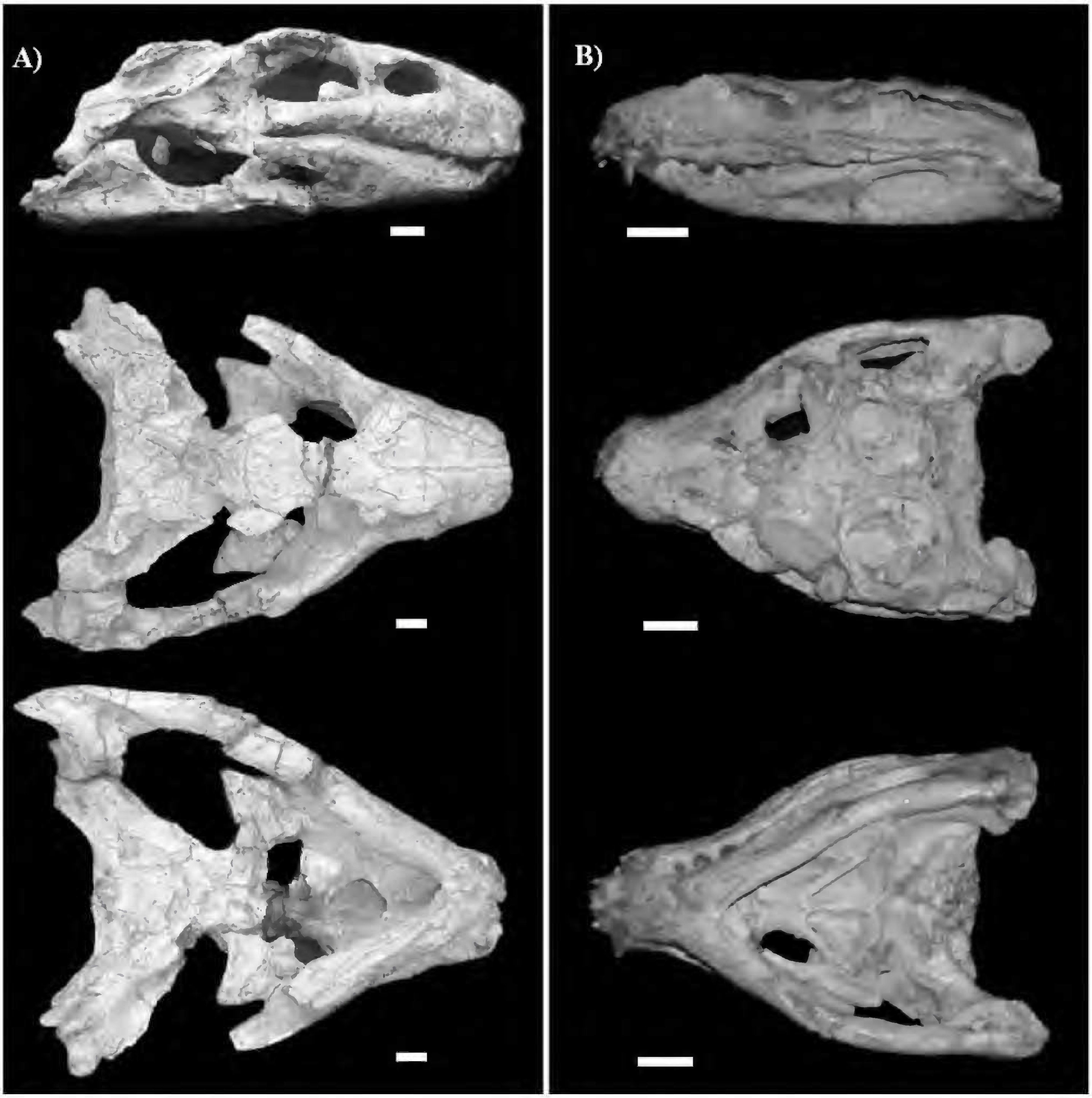

Fig.6- Cranial material of studied specimens, in lateral, parietal and palatal views, showing main similarities between *Notosuchus* and *Mariliasuchus* and main problems of preservation: A) *Notosuchus terrestris* MLP-64-IV-16-5, lectotype, with an abnormally enlarged antorbital fenestra and damaged areas of the skull; B) *Mariliasuchus amarali* URC R•67, with dorsoventral compression. Note the almost triangular outline of the skulls in parietal and palatal views. Bar = 10 mm.

it can be identified at least in MZSP-PV-50. Examination of URC R•67, URC R•68 and the MN specimens allows the recognition of this projection, as originally proposed (Fig.7). The nasal projection is indeed small, not reaching or surpassing the anteriormost (mesial) process of the premaxilla and showing a general outline of a wide triangle, as in *Notosuchus*. *Comahuesuchus* also show the same projection, as seen in MUCPv-202 and MOZ-P-6131 (Bonaparte, 1991; Martinelli, 2003).

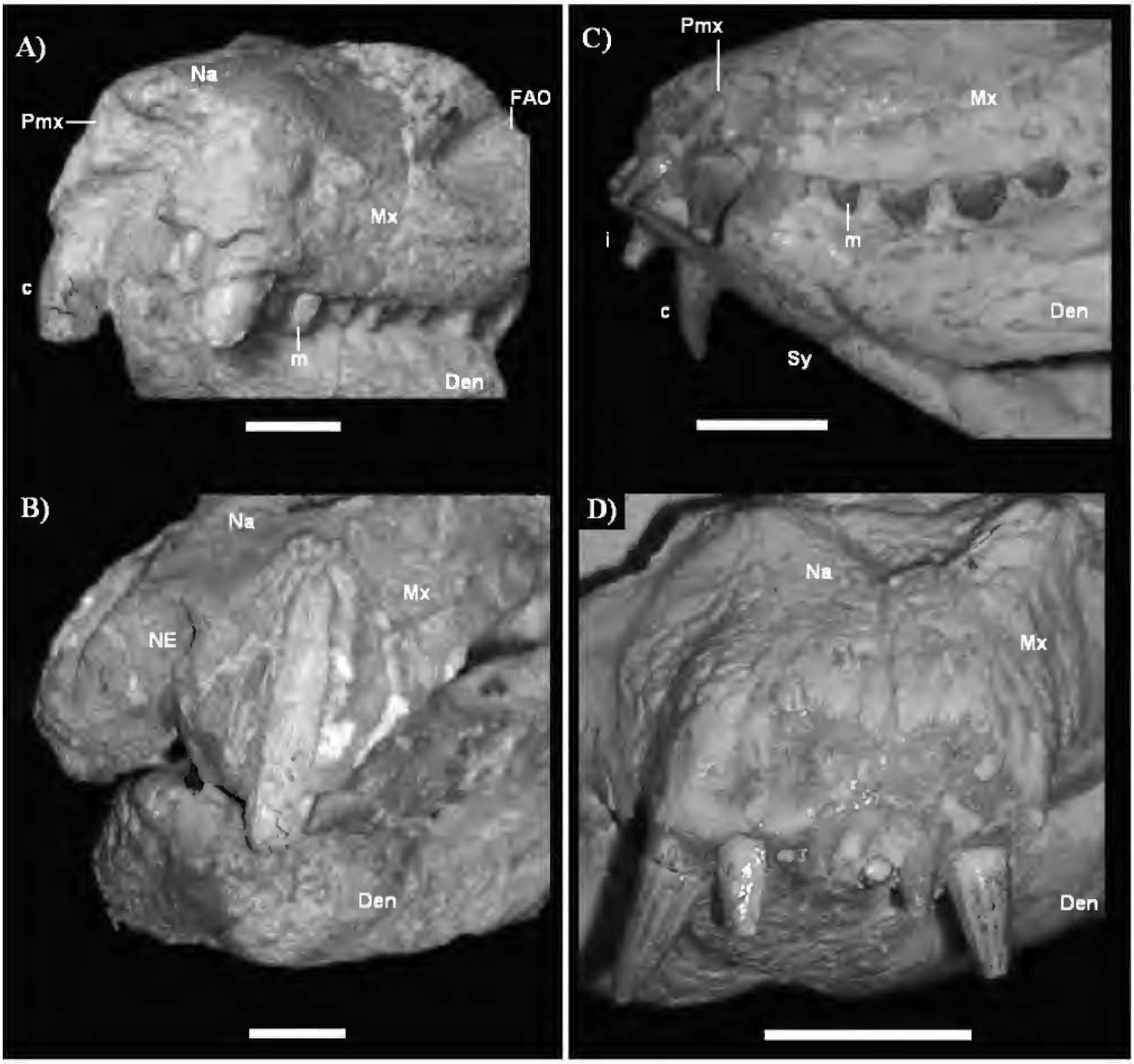

Fig.7- Cranial material of studied specimens, showing the rostrum and its characteristics: A) *Notosuchus terrestris* MACN-Pv-N-24, in anterolateral view; B) MLP-64-IV-16-31(206), in anterolateral view, where the abrasion of the premaxilla exposed the major part of the root from the hypertrophied caniniform; C) *Mariliasuchus amarali* URC R•67, in ventrolateral view, showing the anteriormost dentition and the symphysis; D) *M. amarali* URC R•67, in frontal view, with nasals projecting over the naris in a triangular outline. Note the development of the dorsal part of the premaxilla, lateral to the external naris, which supports the root of the hypertrophied caniniform. Bar = 10 mm.

Palpebrals are poorly preserved in most notosuchians. In *Notosuchus* the presence of two elements over each eye can be verified in a few specimens (MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1119, MPCA-Pv-789). The anterior palpebral is elongated and possibly slightly curved, supported mesially by the prefrontal. The posterior palpebral is short and thick, supported by the post-orbital. Palpebrals can be seen in several specimens of *Mariliasuchus*, including URC R•67 and MN 6756-V. In URC R•67, both palpebrals are present on the left side of the specimen, and in MN 6756-V both anterior and the right posterior palpebrals are preserved. The anterior palpebral is elongated and curved, tapering posteriorly as in *Notosuchus*. The posterior palpebral is subtriangular, widening posteriorly at the contact with the postorbital. Both structures are ornamented and show a gracile laminar structure. In *Candidodon*, only one palpebral is registered, with a morphology very similar to *Notosuchus* and *Mariliasuchus*. Palpebrals are not preserved in *Comahuesuchus*.

JUGAL – Jugal sutures are difficult to be observed in *Notosuchus*, either due to the presence of ornamentation or to abrasion. Nevertheless, it is broadly accepted that the anterior ramus exceeds the orbit and reaches the ventral end of the lachrymal (GASPARINI, 1971; BONAPARTE, 1991, 1996). The anterior ramus is inclined ventrally, as its anterior end is positioned in a more ventral position than the central body of the jugal. The distal end of the posterior ramus is not so easily identified, and BONAPARTE (1991, 1996) did not included this contact in his reconstruction. Nevertheless, in a few specimens (MACN-Pv-RN-1037, MACN-Pv-RN-1048 and MLP-64-IV-16-7) the distal end exceeds de distal end of the laterotemporal fenestra, as in GASPARINI (1971). The jugal ascending process takes part on the postorbital bar. This structure is gracile and is often not preserved (or poorly preserved), displaced from its original position. ZAHER *et al.* (2006; character 142) consider the postorbital bar of *Notosuchus* as vertical and the jugal posterior ramus as not exceeding the laterotemporal fenestra, but none of the well preserved specimens evaluated showed such features. Whenever the postorbital bar is reasonably preserved (MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045), it shows to be posteromedially inclined, with its lower end (jugal ascending process) positioned anteriorly and externally to its upper end (postorbital descending process).

In *Mariliasuchus* the jugal anterior process also extends at least to the anterior border of the orbit, slightly exceeding it (*contra* CARVALHO & BERTINI, 1999). Nevertheless, it does not extend dorsally and does not meet the lachrymal, as reported by ZAHER *et al.* (2006). As a consequence, the maxilla reaches the anteroventral border of the orbit (ANDRADE, 2005; ZAHER *et al.* (2006). The anterior jugal ramus is also inclined ventrally, as in *Notosuchus*. The postorbital bar (with participation of the ascending jugal ramus) is inclined posteromedially and the posterior jugal ramus extends posterior to the laterotemporal fenestra, as described by ZAHER *et al.* (2006). Over the lateroventral surface of the anterior ramus, close to the contact with the maxilla, there is an evident neurovascular foramen, anteriorly directed (ANDRADE, 2005; ZAHER *et al.*, 2006). The foramen is present in all specimens preserving the ramus and can also be identified in *Sphagesaurus* (ANDRADE, 2005), as well as in *Comahuesuchus* (MARTINELLI, 2003; ANDRADE, 2005; ZAHER *et al.* 2006), but it is absent from *Notosuchus* and *Candidodon*.

In *Comahuesuchus*, the jugal anterior ramus extends dorsally and contacts the lachrymal, preventing the maxilla from reaching the orbit, as in *Notosuchus*. This can be seen in MACN-Pv-N-31 and MOZ-P-6131, as reported by MARTINELLI (2003; *contra* ZAHER *et al.*, 2006). As in *Notosuchus* and *Mariliasuchus*, the anterior jugal ramus seems to be inclined ventrally. In *Candidodon* the jugal does not show inclination of the anterior ramus, but the posterior ramus seems to exceed the laterotemporal fenestra and the postorbital bar, partially preserved on the right side of UFRJ-DG-114-R. The postorbital bar has the same posteromedial inclination found in *Notosuchus*, *Mariliasuchus* and most Mesoeucrocodylia (NOBRE & CARVALHO, 2002).

SKULL TABLE – In *Notosuchus*, the parietal surface is mostly narrow and can be defined as a parietal crest, though it does not project dorsally from the skull table and shows a flattened dorsal surface. From its anterior end, the parietal crest develops posteriorly towards the occipital, where it widens and creates part of a broad, crown-like structure, slightly deeper in its center (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991). The crown-like structure is located between the fenestrae and the occipital border, at the parietal-postparietal suture. In *Mariliasuchus*, the surface cannot be characterized as a crest but, as in *Notosuchus*, it is flat and shows at least some degree of ornamentation. In *Comahuesuchus* the parietal surface is reasonably wide, but still narrower than the frontal. In *Candidodon*, the parietal and the frontal are subequal in width, a quite different condition from *Mariliasuchus*, *Notosuchus* and also *Comahuesuchus*. Currently, only *Notosuchus* and *Mariliasuchus* show variability on the morphology of the parietal, though the reduced number of specimens of *Comahuesuchus* and *Candidodon* prevents statements on the variability within these notosuchian clades.

QUADRATE – In *Notosuchus* the quadrate medial dorsal surface is fenestrated in both sides (GASPARINI, 1971; BONAPARTE, 1991), which can be easily identified on MACN-Pv-N-22, MACN-Pv-RN-1037 and MACN-Pv-RN-1048 (Fig.8). MLP-64-IV-16-3 (not MLP-64-IV-16-1, as reported by GASPARINI, 1971) also preserves the quadrate structure and shows such fenestration. These perforations are also present in the MUCPv specimens (FIORELLI, 2005). Furthermore, reconstruction by RUSCONI (1933) suggests the presence of perforations in an unidentified specimen. The fenestration does not follow a specific pattern and morphology can show small differences even in the same individual, as fenestrae may vary slightly in number, size and position. Most other specimens have the quadrate surface not preserved or covered with matrix. Among all skulls where the quadrate is visible and preserved, only MLP-64-IV-16-5(253) and MLP-64-IV-16-31(206) do not show the quadrate fenestrae (Woodward, 1896). These MLP specimens, although composed of entire skulls, show a poor quality of preservation, lacking several structures and details (*e.g.* pos-orbital bar, interchoanal septum, maxillo-palatine fenestrae, palpebrals). It is possible that these specimens may be anomalous, but the scarceness of material without the fenestration and their preservation highly suggests that differences are taphonomic. It seems clear that the fenestrated quadrate was the rule for *N. terrestris*, as this situation is present in a far greater number of well preserved specimens. Furthermore, other specimens (MACN-Pv-N-22, MACN-Pv-N-23, MACN-Pv-RN-1045, MLP-64-IV-16-30), where the quadrate is severely broken, show that this element was highly pneumatic. In *Mariliasuchus*, quadrate fenestrae were identified by Zaher *et al.* (2006) in MZSP-PV-50, as also in UFRJ-DG-106-R (Fig.2). Other specimens do not preserve the region or it is filled with sediment. No other mesoeucrocodylian shows similar quadrate fenestrae, though it should be stated that these fenestrae reached an extreme development in *Notosuchus*.

The quadrate distal end of *Notosuchus* shows an articular condyle with double articulation (Woodward, 1896; Ortega *et al.*, 2000) and the same can be seen in *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006). The medial head is larger than the lateral one, which can be verified at least in the MN, MZSP and UFRJ-DG specimens. In URC R•67 the medial head is not as evident, and the texture of the surface suggests that the bone is slightly damaged in this area. In URC R•69 the medial condyle of the right quadrate is also damaged, but the occurrence of two distinct heads is evident. It is possible that the condition shown by these URC specimens is the result of an incomplete ossification and presence of cartilage in younger individuals, combined with poor preservation. Nobre & Carvalho (2002) describe the quadrate condyle of *Candidodon* with an opposite morphology, with the lateral head larger and rounder, while the medial head is smaller, showing a flatter acute profile. The same profile can be seen in eusuchians. In *Comahuesuchus*, the quadrate condyles are not preserved.

Palate, choanae, and pterygoid – In *Notosuchus*, the naso-oral fenestra (=incisive foramen, *foramen incisivum*) is recognizable also in a few specimens (MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1041), due to its position on the palate and the fact that most specimens are preserved with the mandibles in occlusion. The premaxillary-maxillary suture is also not accessible in palatal view, due to the presence of matrix and/or symphysis. Thus, the position of the foramen relative to the premaxillary-maxillary suture could not be accurately determined in almost all specimens. This can only be seen in MACN-Pv-RN-1040, where the naso-oral foramen can be accessed from the naris.

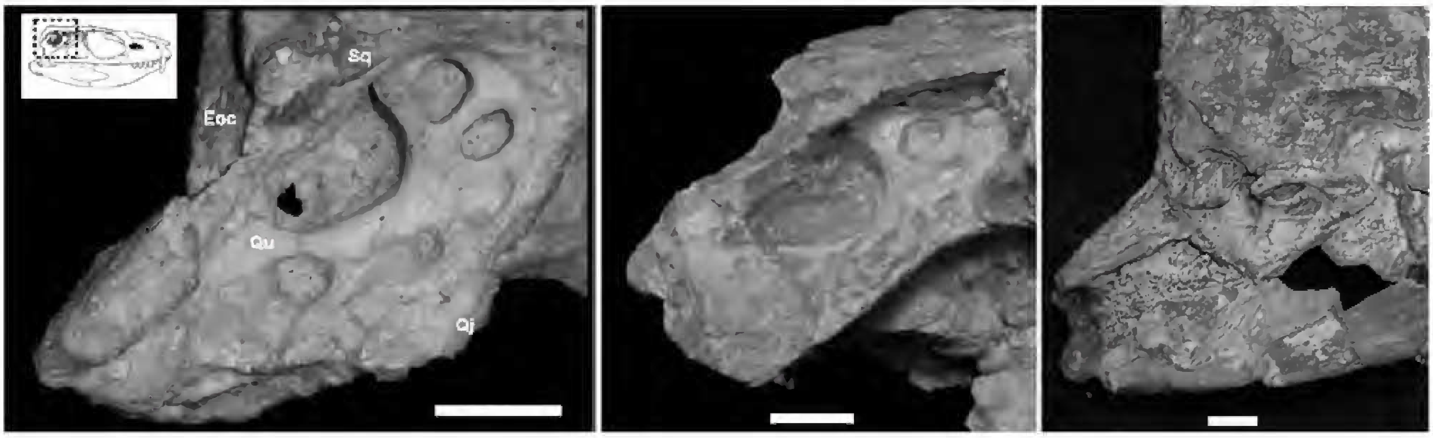

Fig.8- Right quadrate surface in *Notosuchus terrestris*, from specimens MACN-Pv-N-22 (left; dorsolateral view), MACN-Pv-RN-1037 (center; lateral view) and MACN-Pv-RN-1048 (right; dorsal view), showing the characteristic pattern of fenestration. Bar = 10 mm. (skull adapted from Bonaparte, 1991).

It shows a subelliptical profile, similar to a teardrop, and it seems to be limited to the premaxillae. In *Mariliasuchus* the naso-oral fenestra is also hardly accessible, and only four specimens have the area properly exposed. Of these, three specimens (MN 6298-V, MN 6756-V, URC R•68) show an irregular foramen delimited between the premaxilla and the maxilla sutures, while the last, MZSP-PV-50, seems to lack this structure (as reported by Zaher *et al.*, 2006). Reasons for this can be either taphonomic or ontogenetic, and further material is needed to investigate if adult specimens, as MZSP-PV-50, show any trend toward the closure of this structure. Though *Mariliasuchus* and *Notosuchus* show a very different morphology on the naso-oral fenestra, the structure (and the medial surface of the anterior palate) is not preserved either in *Candidodon* or in *Comahuesuchus*, preventing further comparison.

Among mesoeucrocodylians, only *Mariliasuchus* and *Notosuchus* have maxillo-palatine fenestrae (=palatine fenestrae). They constitute small fenestrae positioned near the medial line of the palate (Fig.9), at the suture between palatine and the maxilla (ventral ramus). These structures were identified for the first time by Woodward (1896), in *Notosuchus*. Ever since its original description, the presence of these fenestrae has been widely recognized (Gasparini, 1971; Bonaparte, 1991; Martinelli, 2003; Andrade, 2005; Fiorelli, 2005). Maxillo-palatine fenestrae are almost invariably broken in *Notosuchus*, and this pair of structures appears to be a single one in all specimens studied. Nevertheless, these fenestrae are preserved in MLP-64-IV-16-3 (Woodward, 1971; Gasparini, 1971) and may eventually be observed in other specimens. The anterior borders of these fenestrae do not surpass the fifth pair of teeth anteriorly or the seventh pair, posteriorly.

In *Mariliasuchus*, the recognition of the maxillo-palatine fenestrae came rather later to the description of this taxon. This is due because the holotype has the ventral surface obliterated by rock matrix and it could not be observed in the original description (Carvalho & Bertini, 1999). Maxillo-palatine fenestrae can be seen in URC R•67, URC R•68 (Andrade, 2005), UFRJ-DG-106-R (Vasconcellos & Carvalho, 2005) and also in the MN-UFRJ and MUZUSP specimens (Zaher *et al.*, 2006). In most cases, the actual borders are well preserved, including their medial margins. URC R•68 is an exception and shows only the right fenestra, as the left portion of the palate is not preserved. In UFRJ-DG-105-R the bone surface at the maxilla-palatine contact seems to be damaged and the fenestrae are therefore not clearly visible (as figured in Vasconcellos & Carvalho, 2005). The fenestrae do not surpass the fifth maxillary pair of teeth anteriorly or the sixth pair (last pair) posteriorly.

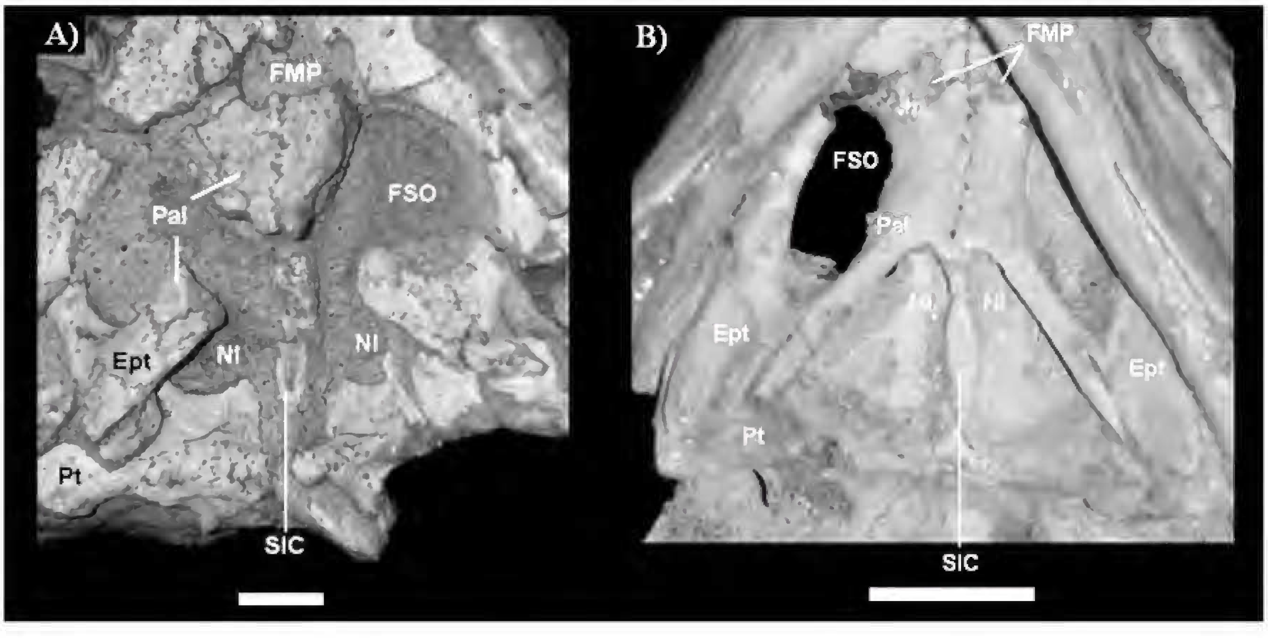

Fig.9- Palatal view of studied material, showing the choanae and perichoanal structures: A) *Notosuchus terrestris* MACN-Pv-RN-1038; B) *Mariliasuchus amarali* URC R•67. Note the the general morphology of the choanae, as the presence of maxillo-palatine fenestrae and interchoanal septum. Bar = 10 mm.

Neither *Candidodon* nor *Comahuesuchus* have these fenestrae or similar structures on the palate (Bonaparte, 1991; Nobre & Carvalho, 2002; Martinelli, 2003), though the area is preserved.

In *Notosuchus* the choanae are ample and triangular (Fig.9), as in Woodward (1896), showing a fragile interchoanal septum (Andrade *et al.*, 2006). The septum is represented, but not commented, by Gasparini (1971; p.90, Plate III-B). Specimens evaluated by Bonaparte (1991) do not preserve the structure. In fact, the MLP series and most of the MACN material do not preserve choanal regions at all, providing no clue to the existence of this structure or to the actual shape of the internal naris. Nevertheless, the interchoanal septum can be identified in MACN-Pv-RN-1038, as an almost complete lamina. Furthermore, MACN-Pv-RN-1045 shows a posterior end of the septum, while MPCA-Pv-789 shows an anterior end. In *Mariliasuchus* choanae are also ample and triangular (Fig.9), as shown by Andrade *et al.* (2006), Zaher *et al.* (2006) and figured by Andrade (2005) and Vasconcellos & Carvalho (2005, 2006). A thin interchoanal septum divides the choanae, as seen in URC R•67 (Andrade, 2005), UFRJ-DG-105-R (Vasconcellos & Carvalho, 2005), MN and MZSP specimens (Zaher *et al.*, 2006). In UFRJ-DG-106-R the septum is incomplete and only its posterior end is preserved (Vasconcellos & Carvalho, 2005). As discussed by Andrade *et al.* (2006), *Comahuesuchus* shows an ample triangular internal naris (Martinelli, 2003), which is consistent with the morphology observed in *Notosuchus, Mariliasuchus* and a few other notosuchians, but the septum itself was not preserved. As observed by Andrade *et al.* (2006), the morphology of the choanae figured by Nobre & Carvalho (2002) for *Candidodon* is rather different from *Mariliasuchus* and *Notosuchus*. This is however an artifact of preservation, since the skull UFRJ-DG-114-R is laterally compressed and the configuration of the pterygoids and the shape of the suborbital fenestra suffered from dramatic deformation. Therefore, the choanae of *Candidodon* still awaits proper characterization.

In *Notosuchus*, the palatine-ectopterygoid contact is of difficult recognition, which is located at the anterolateral border of the choanae (Martinelli, 2003; Andrade *et al.*, 2006). At this point, the palatine posterior process and the ectopterygoid medial process meet, creating a bar that separates the choana from the suborbital fenestra, which can be clearly observed only in MACN-Pv-RN-1038 and MACN-Pv-RN-1040 (Martinelli, 2003; Andrade *et al.*, 2006). In *Mariliasuchus* the situation is rather different from *Notosuchus* (Andrade, 2005; Andrade *et al.*, 2006; Zaher *et al.*, 2006), as the palatine posterolateral processes are long, extending toward the triple contact with the ectopterygoid and the pterygoid, posterior to the suborbital fenestra and lateral to the choanae, as in URC R•67 (Andrade, 2005; Andrade *et al.*, 2006), UFRJ-DG-105-R, UFRJ-DG-106-R (Vasconcellos & Carvalho, 2005), MN and MZSP specimens (Zaher *et al.*, 2006). This contact isolates the pterygoid from the suborbital fenestra. The palatine processes constitute the anterolateral borders of the choanae, with no participation of the ectopterygoid whatsoever. The condition found in *Comahuesuchus* (Martinelli, 2003) truly resembles the one in *Mariliasuchus* and *Sphagesaurus* (Andrade *et al.*, 2006), with palatine and ectopterygoid meeting posteriorly to the suborbital fenestra. The pattern observed in *Notosuchus*, where the palatine and ectopterygoid meet at the palatine bar, can only be seen in baurusuchids (Martinelli, 2003; Andrade *et al.*, 2006; Pinheiro *et al.*, 2008). Nevertheless, in all these cases (including *Sphagesaurus* and baurusuchids), the pterygoid is extensively isolated from the suborbital fenestra. *Candidodon* seems to show a palatine bar, but sutures on this region are still undescribed and it is impossible to state if the palatines have true posterolateral projections, or if the anterolateral borders of the choanae are composed by either the ectopterygoid or the pterygoid (Andrade *et al.*, 2006). Despite de limited information on the taxon, the description by Nobre & Carvalho (2002) seems to suggest that there was no palatine-ectopterygoid contact and the pterygoid reached the posterior end of the suborbital fenestra.

The pterygoid wings (=pterygoid flanges) of *Notosuchus* are usually referred as well developed, as in Woodward (1896) and Gasparini (1971), but they are truly small, when compared to other groups. The pterygoid wings are mostly horizontal and the general structure is robust, though the wings thicken toward the lateral borders and get progressively thinner at the posterior ones. These features can be verified in several specimens of *Notosuchus* (MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1045, MLP-64-IV-16-5, MLP-64-IV-16-7, MLP-64-IV-16-31, MPCA-PV-789/1). In *Mariliasuchus* the pterygoid wings are also proportionally small, and are similar to the ones in *Notosuchus*. These structures are preserved at least in URC R•67, MN 6756-V, MZSP-PV-50, UFRJ-DG-106-R and also partially in MN 6298-V and UFRJ-DG-105-R. However, it should be noticed that both URC R•67 and MN 6756-V show an evident compression, altering the inclination of the ventral flanges. As a character, the pterygoid wings are in fact often coded as small (*e.g.*, Andrade, 2005, character 90; Zaher *et al.*, 2006, character 166). In *Comahuesuchus*, pterygoid wings are poorly preserved.

Nevertheless, they are reasonably small and robust, basically similar to what can be observed in *Notosuchus* and *Mariliasuchus* (Martinelli, 2003; p.562, fig.2). In *Candidodon*, on the other hand, specimen figured by Nobre & Carvalho (2002), shows well developed wings, mostly vertical in orientation. This inclination is however likely to be the result of taphonomic deformation, as UFRJ-DG-114-R is laterally compressed.

Mandible – Whenever the mandible is present in specimens of *Notosuchus*, there are parts missing or deformation. There is no reasonably preserved mandible isolated from the skull, which makes the observation of characters related to the element and its dentition especially problematic. The anterior part of the mandible is constituted by the symphysis, which is concave dorsally (as in Bonaparte, 1991, 1996). Well preserved symphysis showing the inclination upwards (Fig.10) can be seen in specimens with no dorsoventral compression (MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MACN-Pv-RN-1119, MLP-64-IV-16-7, MLP-64-IV-16-24, MLP-64-IV-16-31). In the middle section of the mandible there is a smooth coronoid process, creating an evident dorsal convexity (Woodward, 1896; Gasparini, 1971). In the posterior region of the mandible, the retroarticular process is directed posteroventrally (Woodward, 1896; Gasparini, 1971; *contra* Bonaparte, 1991). In *Mariliasuchus*, at least MN 6756-V and the MZSP specimens have mostly complete mandibles freed from the skull. URC R•68 also shows most of the middle and anterior right hemimandible. In both *Notosuchus* and *Mariliasuchus*, the mandible follows the same general profile. However, it is widely recognized that in *Mariliasuchus* the symphyseal part of the mandible is mostly horizontal (Carvalho & Bertini, 1999; Andrade, 2005; Zaher *et al.*, 2006), while in *Notosuchus* it is inclined dorsally (Woodward, 1896; Bonaparte, 1991; Andrade, 2005). The coronoid process is also present in *Mariliasuchus* and the retroarticular process is directed posteroventrally (Carvalho & Bertini, 1999; Andrade, 2005; Zaher *et al.*, 2006). In *Comahuesuchus* there seems to be a coronoid process, but preservation is imperfect and confirmation must await the description of further specimens. Nevertheless, the profile of the mandible is reasonably different, as the anterior portion of the mandible is wide, shovel-like (Bonaparte, 1991; Martinelli, 2003). In *Candidodon* the only mandible known is distorted and does not show details, although it is possible to recognize that the symphyseal section is narrow and elongated, as in *Notosuchus* and *Mariliasuchus* (Carvalho, 1994).

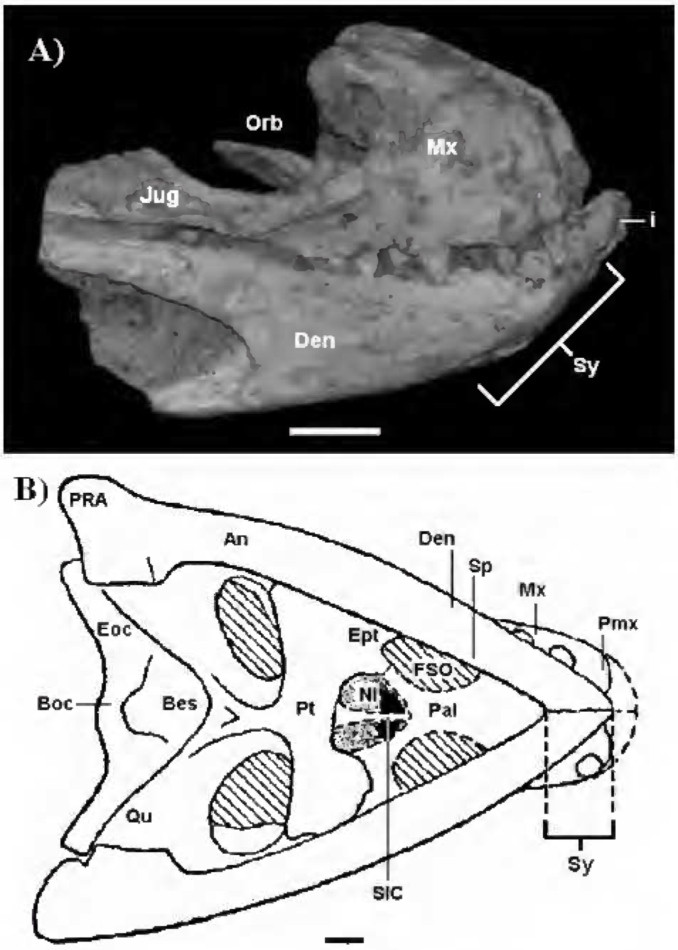

Fig.10- Length of the symphysis in *Notosuchus terrestris*: A) lateral view of the rostrum and mandible of MACN-Pv-N-43, showing the actual length of the symphysis; B) drawing of *N. terrestris* from Price (1959), showing the skull and mandible in ventral view, where the symphysis seems to be shorter than it really is. Reconstruction in "B" based on MLP-64-IV-16-5, lectotype. Note that the reconstruction does not show maxillo-palatine fenestrae, as these structures are not preserved in this specimen. Bar = 10 mm.

In *Notosuchus*, the splenials meet medially. In ventral view, the splenials reach ventrally, marginally taking part of the symphysis. They neither extend anteriorly, nor get fused. At the mandibular ramus, the splenials contribute to the medial border at least to the three posteriormost mandibular alveoli (MACN-Pv-RN-1038, MLP-64-IV-16-13). In *Mariliasuchus*, the splenials relate to the mandible in the same manner. Nevertheless, it is possible to recognize that the splenial contributes to the last four mandibular alveoli (URC R•68, MN 6756-V and MZSP specimens).

Although it is not possible to compare this pattern to the situation in *Candidodon* due to the poor preservation of the mandible, *Comahuesuchus* shows that at least the two posteriormost alveoli receive contribution of the splenial (Martinelli, 2003; p.566, fig.4).

One of the important aspects shown by the reevaluation of the specimens refers to the morphology of the symphysis, which is frequently described as short in *Notosuchus* and *Mariliasuchus* (Woodward, 1896; Price, 1959; Gasparini, 1971; Carvalho & Bertini, 1999; Pol, 2003; Zaher *et al.*, 2006), as in Protosuchia. This may occur with *Notosuchus*, as this species shows a symphysis inclined upwards, a characteristic observed in several specimens (MACN-Pv-N-24, MACN-Pv-N-43, MACN-Pv-N-107, MACN-Pv-RN-1037, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1040, MACN-Pv-RN-1046, MLP-64-IV-16-5 and MLP-64-IV-16-24 and MLP-64-IV-16-31). Available images and reconstructions in ventral/palatal view show an apparently small area of contact between the rami. Thus, the symphysis seems to represent a very small portion of the mandible length, a truly misleading situation (Fig.10). In MACN-Pv-RN-1048 the symphysis is horizontalized by severe dorso-ventral compression and is clearly elongate. Furthermore, definition of the long symphysis is not straightforward and can be presented in a number of ways. Because in notosuchians the mandible may show proal/propalinal movement (Clark *et al.*, 1989; Wu *et al.*, 1995; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006), the position of the symphysis relative to the rostrum is variable, which gives a false idea as how posteriorly it extends. Some specimens of *Notosuchus* show a forward displacement of the mandible, and the symphysis does not cover most of the palate (*e.g.*, MACN-Pv-N-43, MACN-Pv-RN-1038, MACN-Pv-RN-1039, MACN-Pv-RN-1119). In other specimens, the symphysis is preserved in a slightly more recoiled position, and the symphysis ranges from the anterior border of the premaxilla almost to the anterior border of the maxillo-palatine fenestrae (*e.g.*, MACN-Pv-RN-1037, MACN-Pv-RN-1040, MACN-Pv-RN-1041, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-23, MPCA-PV-789/1, MPCA-PV-791). Such displacement is expected, as it is widely agreed that *Notosuchus* was able of mandibular movements (Ortega *et al.*, 2000; Pol, 2003; Zaher *et al.*, 2006). Another similar aspect is that the mandible includes at least five pairs of teeth, as much as *Mariliasuchus* (Andrade, 2005; Zaher *et al.*, 2006) and *Sphagesaurus* (Pol, 2003; Andrade, 2005). Furthermore, in *Notosuchus*, *Mariliasuchus* and *Sphagesaurus* the teeth in the symphysis are disposed in parallel lines. Whenever a specimen of *Notosuchus* shows a different situation, it can be related to preservation problems, such as the deformation or loss of the first and more delicate section of the symphysis. *Comahuesuchus* shows a long symphysis, despite its shovel-like profile. Dental elements are disposed in a very different disposition though, and the symphysis supports at least nine pairs of teeth, set in an arched line. *Candidodon* has a long symphysis (Carvalho, 1994), which probably included parallel lines of teeth. Despite these notosuchians can be considered as having elongated symphysis, neither of these forms discussed above have the extremely elongated symphysis seen in longirostrine mesoeucrocodylians (*e.g.*, thalattosuchians, dyrosaurids, gavialids), which may include 10 or more pairs of teeth (Andrews, 1913; Benton & Clark, 1988; Clark, 1994; Jouve *et al.*, 2006; Pierce & Benton, 2006).

Both in *Notosuchus* and *Mariliasuchus* the glenoid fossa has a close similar morphology, anteroposteriorly elongated and with a general triangular shape, in dorsal view. The posterior margin is very low and poorly delimited (Woodward, 1896; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006). The elongated articular glenoid fossa must have allowed mandibular mobility (Clark *et al.*, 1989; Wu *et al.*, 1995; Ortega *et al.*, 2000; Pol, 2003; Andrade, 2005; Zaher *et al.*, 2006). Thalattosuchians and most neosuchians, on the other hand, have a well delimited posterior margin and are prived from proal/propalinal displacements of the mandible (Andrews, 1913; Benton & Clark, 1988; Clark, 1994; Jouve *et al.*, 2006; Pierce & Benton, 2006, Turner, 2006).

In the posterior region of the mandible of *Notosuchus*, the retroarticular process is directed posteroventrally (Woodward, 1896; Gasparini, 1971; *contra* Bonaparte, 1991), as in *Mariliasuchus* (Carvalho & Bertini, 1999). In both cases, the retroarticular process shows an ample and continuous single surface for muscle insertion (*musculus depressor mandibulae*), which faces medially, posteriorly and dorsally (Fig.11). This can be seen in a representative number of specimens of *Notosuchus* (MACN-Pv-RN-1037, MLP-64-IV-16-5, MLP-64-IV-16-31) and *Mariliasuchus* (URC R•67, MN 6756-V, UFRJ-DG-105-R, UFRJ-DG-106-R and the MUZUSP specimens).

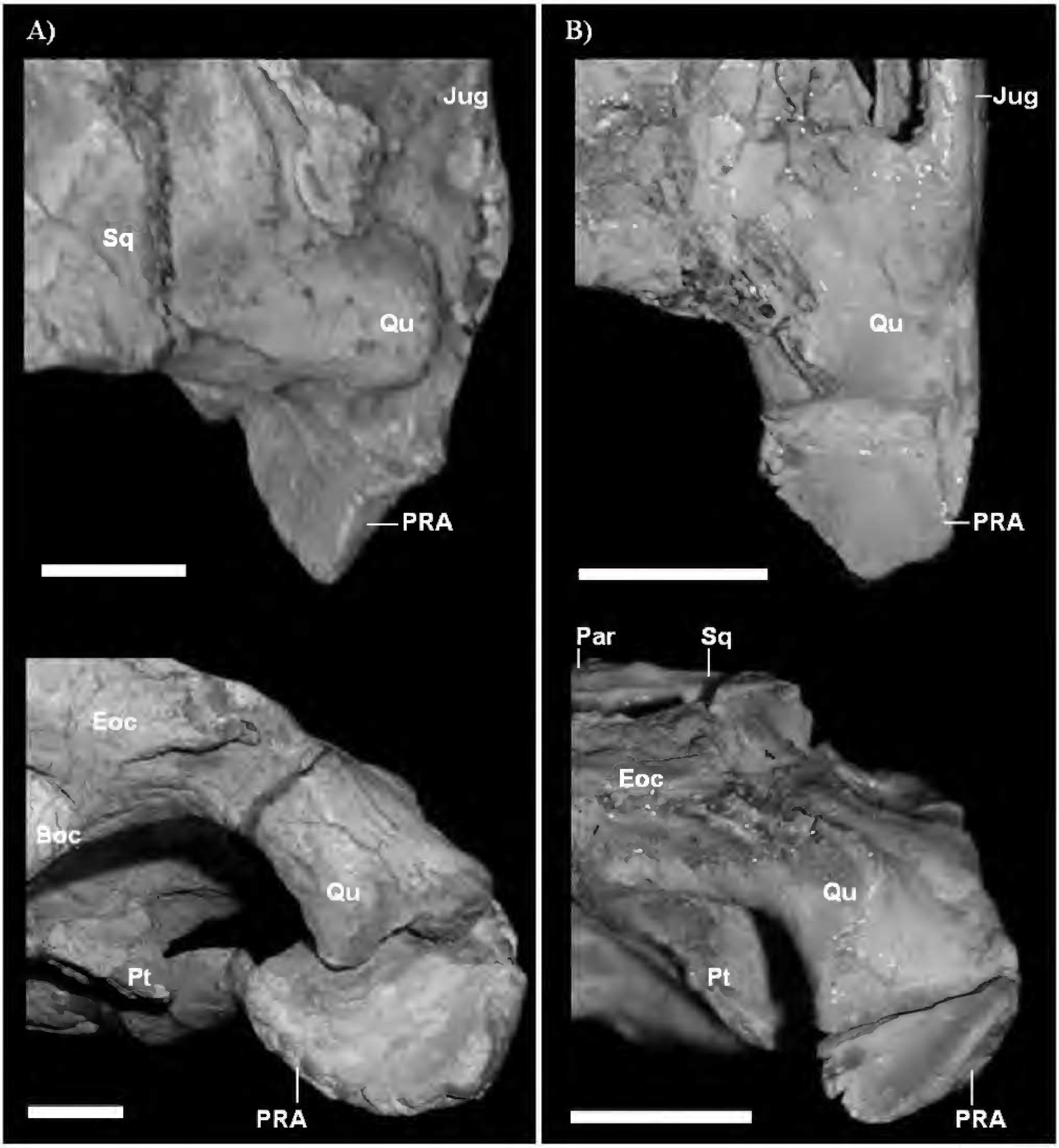

Fig.11- Parietal (top) and occipital views (bottom) of the right retroarticular process from studied specimens: A) *Notosuchus terrestris* MLP-64-IV-16-5, lectotype, where the distal end of the quadrate is broken and slightly twisted; B) *Mariliasuchus amarali* URC R•67, where the medial condyle is incompletely preserved. Bar = 10 mm.

The general shape of this surface is subcircular to subpolygonal, as long as wide. In general aspect, the articular apparatus of *Mariliasuchus* and *Notosuchus* resemble most of the other notosuchians, including the Baurusuchidae. This pattern is clearly different from the elongated and posterodorsally oriented retroarticular process found in Eusuchia, Thalattosuchia and *Sebecus* (ANDREWS, 1913; COLBERT, 1946; BENTON & CLARK, 1988; CLARK, 1994; ORTEGA *et al.*, 2000; PIERCE & BENTON, 2006). Furthermore, at least in eusuchians, thalattosuchians and most neosuchians the retroarticular process have not a single surface, but a lateral surface facing dorsally and a medial surface, facing medially and dorsally, separated by a longitudinal ridge (ANDREWS, 1913; BENTON & CLARK, 1988; CLARK, 1994; PIERCE & BENTON, 2006).

DENTITION – The dentition of *Notosuchus* includes three premaxillary incisiforms, one premaxillary hypertrophied caniniform, one small conic post-caniniform and at least six maxillary molariform teeth in the upper series. In the lower series, possibly 10-11 teeth were present. The first three pair of teeth are small conic and blunt incisiforms. The second and third pairs are preserved in several specimens, but the first pair can only be seen in MACN-Pv-RN-1038 and MACN-Pv-RN-1040. The following tooth is a hypertrophied caniniform, clearly identifiable in most specimens. The first postcaniniform tooth of *Notosuchus* is small and mostly conic, and it is morphologically similar to the premaxillary series, but also blunter and larger. This would allow its characterization as a premolariform tooth. The following teeth are all single cusped molariforms. The premaxilla does not extend far posteriorly to the hypertrophied caniniform, as seen in MACN-Pv-N-24. Specimens show that in most cases there are at least six crowns preserved per maxillae (*e.g.* MACN-Pv-N-24, left crowns from pairs 1-6; MACN-Pv-RN-1037, pairs 1-6 in both sides; MACN-Pv-RN-1038 both sides; MACN-Pv-RN-1040; MLP-64-IV-16-6, pairs 1-6, both sides; MLP-64-IV-16-22, teeth pairs 2 and 3-7 from the right side). A few specimens (MACN-Pv-RN-1041, MLP-64-IV-16-1, MPCA-Pv-789) preserve seven maxillary crowns or their remnants, including the first postcaniniform tooth. However, a posteroventral extension of the premaxilla is noticed at least in MLP-64-IV-16-1 and it is possible to consider that the first post-caniniform tooth occupies an intermediate position between premaxilla and maxilla. It is certain that the premaxilla at least takes part of the anterior alveolar border of the first postcaniniform, providing partial support for the tooth. Nevertheless, it was not possible to identify a single specimen where the premaxilla constituted the entire alveolus. This supports the traditional interpretation of four premaxillary and seven maxillary teeth (WOODWARD, 1896; GASPARINI, 1971; *contra* BONAPARTE, 1991). On the size of the maxillary dentition, the first maxillary tooth was smaller, but the rest of the series had approximately the same size, according to WOODWARD (1896). GASPARINI (1971) considered that the teeth increased in size from the first to the fourth, and the last teeth were similar in size. Reconstruction by BONAPARTE (1991) supports WOODWARD (1897), but shows that the second tooth was also not as developed as the following teeth. Examination of the specimens reveals that maxillary pairs 4-6 seems to be slightly more developed than pairs 2, 3 and 7, but the difference is not as evident as in other mesoeucrocodylians, such as *Araripesuchus*, *Uruguaysuchus* and *Baurusuchus*. Furthermore, development problems may interfere in the interpretation. Nevertheless, the first tooth (the first post-caniniform) is clearly smaller than the fourth tooth.

The dentition of *Mariliasuchus* shows similar number and arrange of teeth, with two premaxillary incisiforms, one premaxillary hypertrophied caniniform, one small conic post-caniniform and six maxillary molariform teeth in the upper series. There are nine teeth in the lower series. The first incisiform is mostly conic. The second premaxillary tooth is also small and conic, but as it is slightly curved it can also be characterized as a caniniform. These teeth are preserved at least in URC R•67 and the MUZUSP specimens, but not in URC-R•68 and the MN material. The third tooth is a hypertrophied caniniform, well preserved in most specimens. The first postcaniniform tooth of *Mariliasuchus* is small and mostly conic, but with a discrete distal curvature of the apex. The second postcaniniform tooth is also small, conical and slightly curved, indicating an intermediate between the anterior element and the following teeth. As described by ZAHER *et al.* (2006), this tooth has the labial side more convex than the lingual side, as all posterior elements. Furthermore, it is stouter and blunter than the anterior teeth. Both the first and the second postcaniniform teeth can thus be characterized as premolariform teeth, due to its intermediate morphology between the typical caniniform and the molariform types.

The third and subsequent postcaniniform teeth are all clearly molariform. The fourth postcaniniform tooth is the most developed within the series, and the last element is clearly the smallest of the maxillary series. As in *Notosuchus*, the premaxilla also does not extend far posteriorly to the hypertrophied caniniform in lateral view, as observed in URC R•67, URC R•68 (Andrade, 2005) and the MN specimens, but also as reported for the holotype (Carvalho & Bertini, 1999). In URC R•68 it is possible to recognize that the premaxilla extend distally in ventral aspect, taking part of the anterior portion of the alveolus (Fig.12). This extension and the borderline participation can also be verified in Zaher *et al.* (2006; fig.9B, p.20) for MZSP-PV-51, and seems to be present in MZSP-PV-50 (Zaher *et al.*, 2006; fig.5, p.9). Nevertheless, Zaher *et al.* (2006) prefer to consider that the first postcaniniform is included entirely in the premaxilla. Though the first postcaniniform tooth is small, the premaxilla extension is not as high as it should be to produce an effective support, and the maxilla certainly plays an important role in bearing this element. Furthermore, there is no evidence supporting that the maxilla is entirely excluded from the alveolus. Despite differences of interpretation, it seems clear that divergences on the position of the first postcaniniform tooth are due to the same reasons in *Notosuchus* and *Mariliasuchus*. The first postcaniniform tooth is, in both cases, partially held by the premaxilla and the maxilla, is mostly conical and less developed than the surrounding elements of the upper series, showing an intermediate morphology between caniniform and molariform.

Regarding the mandibular dentition, observation of MACN-Pv-RN-1038 suggests 11 mandibulary teeth in an occluded position, with crowns pairs 1-2 (left side) mildly procumbent. MLP-64-IV-16-14 shows small right anterior mandibulary tooth (pair 2?) with an elliptic cross-section, congruent with the presence of procumbent anterior teeth. Other specimens do not preserve anterior teeth or do not show them, albeit it should be observed that the anterior section of the mandible is inclined upwards, and any tooth that occludes with the premaxillary series is expected to be slightly procumbent to adequately occlude with the ones in the upper series. Though *Notosuchus* provides only a limited amount of information on its mandibulary dentition, there is no evidence for caniniform teeth whatsoever, and the anterior teeth were incisiform, while posterior teeth were molariform. The skull with associated mandible MACN-Pv-RN-1038, the right hemimandible MLP-64-IV-16-13 and the partial skulls MLP-64-IV-16-1 and MLP-64-IV-16-22 (where matrix associated to the palate beautifully holds the cross-section of mandibulary crowns) seem to support at least 10 mandibulary teeth. In *Mariliasuchus* the mandibular dentition shows a better preservation than in *Notosuchus*, for all specimens analyzed. As in *Notosuchus*, no element of the mandibular series of *Mariliasuchus* can be characterized as a caniniform, due to the complete lack of medial/distal curvature of the apex (URC R•68, MN 6756-V, MUZUSP specimens). The first five elements are progressively more procumbent anteriorly.

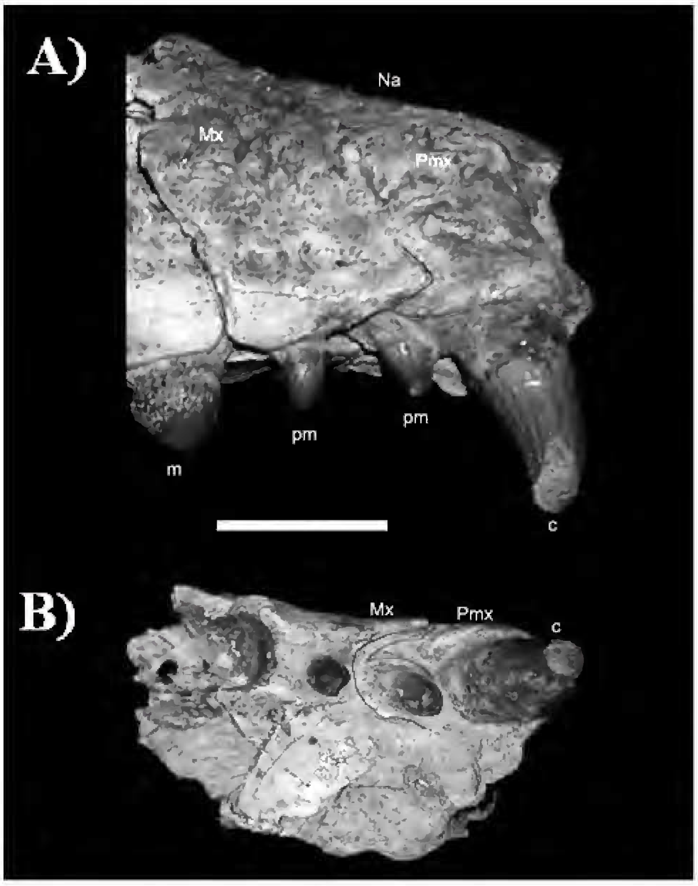

Fig.12- Anteriormost portion of the rostrum in *Mariliasuchus amarali*, specimen URC R•68, showing the contribution of the premaxilla and maxilla to the first maxillary alveolus: A) lateral view; B) palatal view. Dark lines represent the limits for each element, showing that the alveolus of the first postcaniniform receives contribution from both the premaxilla and the maxilla. Note the intermediate morphology shown by the first two postcaniniform teeth and also the evident molariform morphology shown by the third postcaniniform tooth. Bar = 10 mm.

The dentition is procumbent anteriorly, where the anteriormost elements are small and mostly conical (incisiform), and the postcaniniform teeth progress to a typical molariform pattern. There is no evident distinction though, as the fourth and fifth teeth from the lower series do not show either the typical incisiform or molariform morphology.

The morphology of the anteriormost mandibular dentition of *Mariliasuchus* is highly characteristic, because combines procumbent alveoli and straight anterior teeth. The result is that the crowns of the first pair of mandibulary teeth are almost horizontal. In *Notosuchus*, the anterior teeth are procumbent, but are not horizontal as in *Mariliasuchus*, as seen in MACN-Pv-RN-1038, MLP-64-IV-16-14. Furthermore, these specimens suggest the existence of a small toothless area at the anteriormost section of the mandible. The presence of this diastema between the right and the left series is not certain though, and observation of further material is needed to exclude taphonomic alteration.

An important aspect of the dental morphology of *Mariliasuchus* and *Notosuchus* is the peculiar occurrence of hypertrophied caniniforms in these clades, when compared to other notosuchians. Each of these caniniforms is particularly robust, tusk-like and firmly attached to the premaxilla, with roots extending through the maxillary bone to the upper part of the rostrum, where a thickened, well ornamented area can be identified (Fig.7). There is only a mildly enlarged caniniform in the premaxilla of *Candidodon* (Nobre & Carvalho, 2002), but it is not as developed as in *Mariliasuchus* and *Notosuchus*. The premaxillary dentition of *Comahuesuchus* does not show evidence of hypertrophied or even slightly enlarged teeth (Bonaparte, 1991; Martinelli, 2003). Truly hypertrophied caniniforms were certainly present in the premaxilla of *Sphagesaurus*, *Malawisuchus*, highly predaceous forms such as baurusuchids and other mesoeucrocodylians (Price, 1945; Gomani, 1997; Riff & Kellner, 2001; Pol, 2003), but are also absent from *Simosuchus* and thalattosuchians (Andrews, 1913; Buckley *et al.*, 2000). A more peculiar aspect of *Mariliasuchus* and *Notosuchus* is the lack of hypertrophied caniniforms from the maxilla. Such teeth are present in most mesoeucrocodylians and are usually compressed laterally, even acquiring a blade-like profile. The maxillary hypercaniniform is extremely well developed in *Candidodon* and baurusuchids (Riff & Kellner, 2001; Nobre & Carvalho, 2002). *Comahuesuchus* also shows a hypertrophied maxillary caniniform, although not as extremely developed as in the previous forms (Bonaparte, 1991; Martinelli, 2003). Well developed caniniforms can also be found in *Malawisuchus*, *Uruguaysuchus*, most eusuchians and several neosuchians (Benton & Clark, 1988; Clark, 1994). Nevertheless, such elements are absent from *Sphagesaurus*, *Chimaerasuchus*, *Simosuchus*, most thalattosuchians and longirostrine forms (Andrews, 1913; Wu & Sues, 1996; Buckley *et al.*, 2000; Pol, 2003). One pair of mandibulary hypertrophied caniniforms is also usually found in mesoeucrocodylians, as also in more basal groups of crocodylomorphs and in almost all eusuchian genera (Benton & Clark, 1988; Clark, 1994). Whenever present, they occlude where the premaxillary-maxillary suture lies. The only exception is *Comahuesuchus*, as in this form the mandibular hypercaniniform occupy a rather posterior position, fitting the paracanine fossa (Bonaparte, 1991; Martinelli, 2003). In *Candidodon* the condition is unknown, due to the preservation of the mandible. These caniniforms are only absent from *Mariliasuchus* and *Notosuchus*, as well as a few other clades (*Sphagesaurus, Chimaerasuchus*, longirostrine mesoeucrocodylians). In overview, only a few mesoeucrocodylians truly show the same pattern of disposition of hypertrophied caniniforms (i.e. restricted to the premaxilla, as in *Notoshuchus* and *Mariliasuchus*). These are *Sphagesaurus*, *Adamantinasuchus* and possibly *Chimaerasuchus*. In all other taxa, either there is no hypercaniniform at all (thalattosuchians, longirostrine forms) or there are hypertrophied caniniforms in the maxilla and the mandible.

Root morphology and teeth implantation – In *Notosuchus*, no tooth shows a basal crown constriction, although distinction between root and crown is evident (MACN-Pv-RN-1038). Roots, whenever exposed, were conic to elliptic in cross-section, and never divided. Woodward (1896; p.12, 1st§) found no successional tooth in the MLP series, which are not reported also by Gasparini (1971) or Bonaparte (1991). No single specimen studied shown reposition teeth, even though some specimens (*e.g.*, MACN-Pv-RN-1038, MLP-64-IV-16-31) had lingual or labial abrasions exposing roots of premaxillary and mandibulary teeth. In *Mariliasuchus*, middle and posterior teeth have a clear constriction identifying the limits between root and crown. Roots are undivided, what can be accessed in URC R•68. Reposition teeth have also never been reported in *Mariliasuchus*, and URC R•68 does not show any evidence of them. Oblique implantation can be observed in *Notosuchus* and

Mariliasuchus (Fig.13). This condition was observed for the first time by Woodward (1896), who identified oblique teeth in the maxilla of *Notosuchus*. Oblique teeth are always molariform and this can be better observed in the maxillae of MACN-N-22, MLP-64-IV-16-1, MLP-64-IV-16-6, MLP-64-IV-16-7, MLP-64-IV-16-11, MLP-64-IV-16-16, MLP-64-IV-16-22, MLP-64-IV-16-23 and MPCA-PV-789/1 (Fig.13). Oblique implantation on the dentary can be well observed in MLP-64-IV-16-13 (Fig.13B), but also in MLP-64-IV-16-1 and MLP-64-IV-16-22. Most of these specimens are fragmentary, but helpful to access the character. Oblique implantation is also present in *Mariliasuchus*, which can be easily observed in URC R•68. Nevertheless, oblique implantation is not present in all molariforms and certainly does not affect the premolariforms. Although there is intraspecific variability (Zaher *et al.*, 2006), oblique implantation can easily be identified in at least a part of the postcaniniform teeth pairs 3-5 (URC R•68, MN and MUZUSP specimens) and mandibulary pairs 6-8 (URC R•68, MN 6756-V, MUZUSP specimens). None of the analyzed specimens lacks oblique teeth and these are present also in the MUZUSP specimens. The displacement is always paramesial and bilateral, affecting teeth with wear surfaces, indicating that this arrange is not accidental and due to a taphonomic bias. The occurrence of oblique implantation in *Mariliasuchus* and *Notosuchus* may only be compared to *Sphagesaurus*. In all other cases, teeth have a more common disposition, with carinae parallel to the maxillary/mandibulary alveolar margin. No single tooth of *Candidodon* shows oblique implantation whatsoever (Nobre & Carvalho, 2002), as in *Comahuesuchus*.

Ornamentation, carinae, and wear surfaces – Ornamentation is present in *Mariliasuchus* teeth, constituting a series of well developed basal-apical undivided ridges in anterior teeth and a fabric of small anastomosed ridges over the teeth surface (Andrade, 2005; Andrade & Bertini, 2005b; Zaher *et al.*, 2006). Small true denticles constitute carinae, which develop on mesial and distal surfaces of middle and posterior teeth only, but never on the anterior teeth (Andrade & Bertini, 2005b). Zaher *et al.* (2006) prefers to consider these as small tubercles rather than true denticles, but without using scanning electronic microscopy. Both Andrade & Bertini (2005b) and Zaher *et al.* (2006) agree that these structures are tubercle-like and do not match the morphology found in ziphodont dentition. As identified by Andrade (2005) and Zaher *et al.* (2006), anteroposteriorly elongated wear surfaces are present in maxillary and middle and posterior mandibulary teeth. These are inclined lingually and distally in maxillary teeth and labially and mesially in matching mandibulary elements. Wear surfaces can also be seen in the tips of the hypertrophied caniniform and the first postcaniniform tooth. In both cases, wear surfaces are subelliptical and face mesially and ventrally (Andrade, 2005). In *Notosuchus* the situation is more elusive, as just a few specimens preserve traces of the tooth surface.

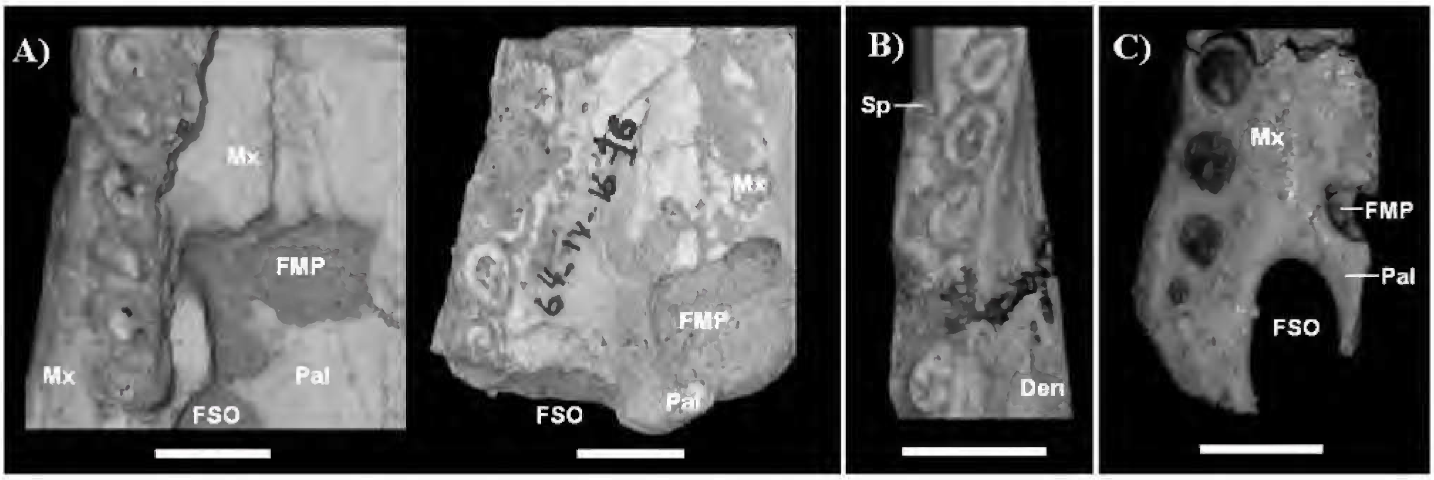

Fig.13- Cranial material of the specimens studied, showing the oblique implantation of the maxillary and dentary teeth: A) rostrum of *Notosuchus terrestris* in palatal view, specimens MLP-64-IV-16-1 (left) and MLP-64-IV-16-16 (right); B) *N. terrestris* MLP-64-IV-16-13, dorsal view of the right ramus of the mandible; C) *Mariliasuchus amarali* URC R•68, in palatal view. Bar = 10 mm.

The presence of ornamentation, carinae and wear surfaces needs further documentation and support. *Notosuchus* is usually considered as possessing carinae (Prasad & Broin, 2002; Zaher *et al.*, 2006, character 120). Woodward (1896) identified flutings in specimen 241 (Woodward, 1896; Pl.2, Fig.5), corresponding to ornamentation. Only MACN-Pv-N-23 preserves remnants of basal-apical ridges on the labial side of the fourth(?) and the sixth(?) maxillary crowns, from the right maxilla (Fig.14). These appear as undivided strong ridges, rather than the light anastomosed pattern seen in *Mariliasuchus*. Woodward (1896) recognized "a feeble crenulation" on the anterior edge of the seventh mandibulary tooth of specimen 200 (Woodward, 1896; p.12, 1st§; Pl.2, Fig.4a), but also on the distal face of the maxillary molariforms. This suggests the presence of denticulated carinae for *Notosuchus*, but the specimens are lost and no evidence truly supports this information. Nevertheless, Woodward's (1896) work is the first description of such features, matching posterior descriptions of denticulated carinae in other taxa and is highly unlikely to be biased. *Notosuchus* may also have shown wear surfaces, what is consistent with proal/propalinal jaw movents. According to Woodward (1896; p.12, 1st§) "the eight and tenth (maxillary) teeth seem to exhibit an outer oblique facette worn by opposing teeth from the upper jaw", in specimen 200. Once more, lack of preservation hinders the appropriate identification of these surfaces.

Both *Mariliasuchus* and *Notosuchus* show heterodonty in a peculiar pattern. The anteriormost teeth are small incisiforms and the last premaxillary tooth is a hypertrophied caniniform (Fig.7). The posterior elements of the upper series are followed by 1-2 teeth with intermediate morphology ("premolariforms"), and these are followed by molariform teeth that increase and then decrease in size posteriorly. Furthermore, the premaxilla and the maxilla contribute to the alveolus of the first postcaniniform tooth and to the support of this element, which is clearly not the case for either *Comahuesuchus* or *Candidodon*. In a broad view, the dentition of *Mariliasuchus* and *Notosuchus* resemble each other much more than to *Comahuesuchus* or *Candidodon*. In this last notosuchian an additional and important difference is that molariform teeth are cingulate and lack completely the denticulated carinae.

Fig.14- Tooth ornamentation in *Notosuchus terrestris* MACN-Pv-N-23. Note the presence of basal-apical undivided crests partially preserved on the labial surface of the fourth(?) and the sixth(?) molariforms from the right maxilla, indicated by white pointers.

Furthermore, in *Candidodon* there are at least three pairs of maxillary caniniforms, one of them clearly hypertrophied. In the premaxilla, the most developed tooth is proportionally not as developed as in *Notosuchus* and *Mariliasuchus*. In *Comahuesuchus* the teeth may be all single cusped, but there are no molariforms and hypertrophied caniniforms can only be found in the maxilla and posterior part of the mandible, exactly the opposite pattern shown by *Mariliasuchus* and *Notosuchus*. There is no evidence for ornamentation or carinae in the teeth of *Comahuesuchus* (Bonaparte, 1991), though preservation bias may have severely compromised observation of these features in the very few specimens known.

Comparative evaluation of the dentition shows that at least for this parameter, *Candidodon* and *Comahuesuchus* are not similar forms. *Sphagesaurus* shows to be a much better correlated. The dentition of this mesoeucrocodylian also shows only one pair of hypertrophied caniniforms in the premaxilla and none in the maxilla/mandible, predominance of molariform teeth, presence of obliquely implanted teeth, procumbent dentition in the anterior part of the mandible and all teeth single cusped and intensely ornamentated (Price, 1950; Pol, 2003; Andrade, 2005; Andrade & Bertini, 2007). In fact, the dentition of *Sphagesaurus* is much more similar to the dentition of *Notosuchus* and *Mariliasuchus* than the dentition of *Comahuesuchus* or *Candidodon*. The most important differences of *Sphagesaurus* from *Notosuchus* and *Mariliasuchus* are the absence of precaniniform teeth in the premaxilla, a more clearly distinction between caniniforms and molariforms and a more extreme paramesial rotation of middle and posterior teeth. Even though, in *Mariliasuchus*, *Notosuchus* and *Sphagesaurus* all the maxillary teeth are robust, ornamented, single cusped and distinctly modified to process food, rather than for prey capture. Furthermore, *Sphagesaurus* shows wear surfaces and was capable of anteroposterior mandibular movements (Pol, 2003). *Chimaerasuchus* also have most of these features, but the teeth are not as robust, showing multicusped wider crowns and lack ornamentation (Wu *et al.*, 1995; Wu & Sues, 1986). *Simosuchus* has spatulated teeth and broad jaws (Ortega *et al.*, 2000), but is hardly comparable to any other taxon. Most remaining mesoeucrocodylians show at least the anterior maxillary and middle mandibulary teeth caniniform curved, as in *Araripesuchus*, *Candidodon* and *Uruguaysuchus*.

Variable parietal morphology: a special case in Mesoeucrocodylia?

In *Notosuchus*, the parietal crest can be present in two forms (Fig.15). As in the *Notosuchus* lectotype, the crest widens progressively from its anterior end to the crown, producing an elongated triangular outline. On the other hand, the parietal crest can be narrow throughout and only widens very rapidly near its end, close to the crown, as in MACN-Pv-RN-1037. This creates a paddle-shaped, constricted crest with a subcircular crown. In the first morphological type, the crown and the crest are continuous, while in the second type the crown is completely distinct from the crest due to a constriction. Because of the relation between the crest and the supratemporal fenestra, in the paddle-shaped type of crest there is more area for muscular fibers to attach on the mesial border of the fenestra, though the difference is hardly noticeable. There is no correlation between the presence of this constriction (determining the paddle-shaped crest) with geographical and stratigraphical provenance, as the different morphologies are present in individuals of all collections. This constriction is also not related to preservation, as it occurs both in well preserved and poorly preserved specimens, and it cannot be related to ontogenesis, as it occurs in adult and semi-adult specimens.

These are discrete states present in *Notosuchus terrestris*, with no intermediate stages. The paddle shaped type of crest can be identified in approximately 50% of the specimens evaluated (Tab.2). Due to its bimodal distribution, the variability of parietal morphology may represent the first reasonable evidence for sexual dimorphism in mesoeucrocodylians. Nevertheless, a larger sample is desirable to support the hypothesis, and a more careful exploration of the subject is needed for *Notosuchus*.

As mentioned previously, Zaher *et al.* (2006) report variability in the morphology of parietal of *Mariliasuchus* MZSP-PV-51. Examination of specimens and observation of main bibliographic references (Vasconcellos & Carvalho, 2005, 2006; Zaher *et al.*, 2006) indicate that MN 6298-V, MZSP-PV-50, URC R•67 have a much narrower parietal, while MZSP-PV-51, MN 6756-V and UFRJ-DG-106-R show a proportionally wider surface. In all cases, the parietal surface is flat and the medial borders of the supratemporal fenestrae show the same curved profile.

Nevertheless, considering the number of specimens, it is not possible to evaluate if the variable character is truly discrete or may be part of a continuous series. Although the small sample is insufficient to avoid the risk of accidental distribution, it is possible that this represent another true example of sexual dimorphism in Notosuchia, as discussed by Zaher *et al.* (2006). If confirmed in both *Mariliasuchus* and *Notosuchus*, the occurrence of sexual dimorphism may constitute further evidence of close relationship between these species. Furthermore, the possible existence of this variability in these taxa suggests that other species of notosuchians might show the same trait.

PHYLOGENETICAL RELATIONSHIPS OF *MARILIASUCHUS AMARALI* AND *NOTOSUCHUS TERRESTRIS* WITH OTHER SOUTH AMERICAN NOTOSUCHIANS

Methodology applied

A preliminary analysis focusing on notosuchians (Appendix 1) was carried out. The objective was to verify the relationships of *Notosuchus*, *Mariliasuchus*, *Candidodon* and *Comahuesuchus*. This analysis used characters from several previous contributions (Benton & Clark, 1988; Clark, 1994;

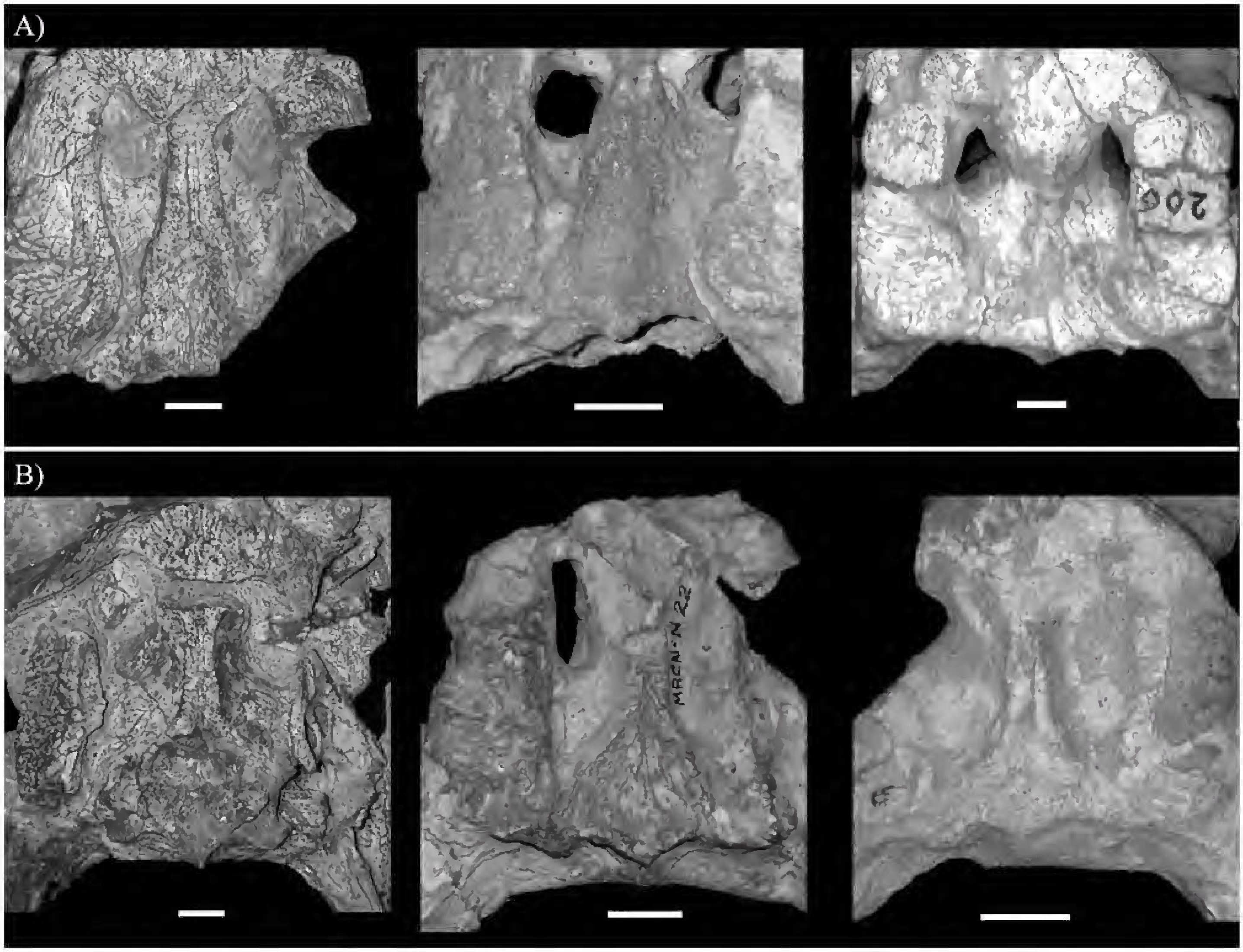

Fig.15- Morphological variation in the parietal of *Notosuchus terrestris*, in dorsal view. A) Triangular crest in MACN-Pv-RN-1045 (left), MACN-Pv-N-107 (center) and MLP-64-IV-16-31(206) (right); B) Paddle-shaped crest in MACN-Pv-RN-1048 (left), MACN-Pv-N-22 (center) and MLP-64-IV-16-8(209) (right). Note that both morphologies are present in material from Rio Negro (left) and Neuquén (center and right) provinces. Note also that both morphologies occur in MACN (center and left) and MLP (right) specimens. Bar = 10 mm.

TABLE 2. Intra-specific variability in the morphology of the parietal crest in *Notosuchus terrestris*.

	TRIANGULAR CREST	PADDLE-SHAPED CREST
Rio Negro	MACN-Pv-RN-1045, MACN-Pv-RN-1119	MACN-Pv-RN-1037, MACN-Pv-RN-1041, MACN-Pv-RN-1048, MACN-Pv-RN-1118
Neuquen	MACN-Pv-N-23, MACN-Pv-N-107, MLP-64-IV-16-1, MLP-64-IV-16-3, MLP-64-IV-16-6, MLP-64-IV-16-31	MACN-Pv-N-22, MLP-64-IV-16-8, MLP-64-IV-16-10
Total	8	7

Note that (i) specimens from MACN and MLP show both types of crests; (ii) specimens from Rio Negro (MACN-Pv-RN) and Neuquén (all others) also show both types of crest.

WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; MARTINELLI, 2003; POL, 2003; SERENO *et al.*, 2003), but also from the unpublished analysis of ANDRADE (2005) (Appendix 2). Baurusuchidae terminal includes information from *Baurusuchus pachecoi* and *Stratiotosuchus maxhechti*. *Uruguaysuchus* refers only to *U. aznarezi*, as *U. terrai* is considered a possible junior synonym to the former (ANDRADE, 2005; ANDRADE & BERTINI, 2005a). The matrix included 20 terminals and 183 characters (Appendix 3).

Phylogenetic analysis (HENNIG, 1966) was carried out with PAUP 4.0b10 (SWOFFORD, 2002), using heuristic search (10,000 replicates). All characters were treated as unordered, with equal weight, and assuming the shortest optimization possible between accelerated and delayed transitions. These options were adopted to avoid the influence of *a priori* assumptions in the analysis. The collapse option for zero length branch was applied. Bootstrap (FELSENSTEIN, 1985) and branch decay (BREMER, 1994) were used to evaluate the tree stability. Bootstrap used 200 replicates. Branch decay was calculated with the use of TreeRot (SORENSON, 1999).

Due to the preliminary character of this analysis, a second analysis using a different framework was done to support or disprove results presented here. The matrix presented by ZAHER *et al.* (2006) was selected because it included a larger number of terminals and a good representation of the notosuchian clades. The original matrix by ZAHER *et al.* (2006) was based on an extended version of POL & NORELL (2004b), with the addition of seven characters, composing a matrix with 46 terminals and 198 characters (Appendix 4). A preparatory analysis using the original dataset was done to check for potential problems, using the same options provided by ZAHER *et al.* (2006), including the exclusion of character 5. The analysis of the original dataset by ZAHER *et al.* (2006) failed to achieve the same results in all attempts, obtaining a strict consensus that is three steps shorter (655 steps, from originally 658 steps), but otherwise identical to the original topology. Alternate analysis of the same dataset shows that the original number of steps could only be achieved if the character 5 was included in the analysis, without alteration of the topology and recovering the same indexes presented by ZAHER *et al.* (2006). It was understood that the original dataset was performing appropriately, but it is possible that the original analysis shown by ZAHER *et al.* (2006) actually included character 5.

The original dataset was then modified according to morpho-anatomical observation of the specimens. This modified version of the dataset has undergone three steps of progressive modifications, to ensure adequate comparison with the original results. In the first step, the dataset was subject to a detailed revision focused on the data coding of *Notosuchus*, *Mariliasuchus*, *Comahuesuchus*, *Candidodon* and *Sphagesaurus* (Appendix 5). Revision of *Candidodon* included basic morphological information on cranial data, obtained from CARVALHO (1994) and NOBRE & CARVALHO (2002), but not used by ZAHER *et al.* (2006). Revision of other taxa followed the morpho-anatomical observations addressed in this study, also reducing the number of missing data, with minor corrections introduced to *Malawisuchus*, *Uruguaysuchus* and both *Araripesuchus* species (Appendix 5). Characters coded as ordered were also revaluated and a reduced list produced, with the exclusion of few characters (1, 3, 65, 67, 105, 107 and 143) that were not considered to be orderable. This dataset was then used to run an unordered analysis. Ordering and successive weighting were applied only to verify stability and increase resolution.

A second step used the modified matrix, from where characters were excluded to verify the influence of these components over the original topology presented by Zaher *et al.* (2006). Only six characters were excluded, related to dentition (105, 107, 120, 192, 194) and jugal morphology (193) (Appendix 4). This dataset was then used to run an unordered analysis.

In the third step of the modified phylogenetic analysis by Zaher *et al.* (2006), the information from the characters excluded in step two (105, 107, 120, 192, 194) was reintroduced with restructured characters (Appendix 6). This dataset (Appendix 7) was then used to run an unordered analysis.

Successive weighting (Farris, 1969) was applied to unordered analysis as an exploratory method, to evaluate the stability and the limits of the topology. Ordered analysis was used in the same way, to evaluate stability and congruence but only applied to a restricted number of characters, with the modified dataset from Zaher *et al.* (2006). Bootstrap (100 replicates) was also used to evaluate tree stability only in the third (final) step of the second analysis.

Ordering and character exclusion from modified matrix of Zaher *et al.* (2006)

Besides general criticism eventually presented against the use of ordered series, Wagner parsimony (Farris, 1970) was considered inapplicable for seven characters (1, 3, 65, 67, 105, 107, 143) from Zaher *et al.* (2006) (Appendix 4). With exception of taxa listed in Appendix 5: (i) the original coding applies for the first step of the second analysis; (ii) the original coding was completely excluded from the second and third steps; (iii) revised coding with corrected information was only used in the third step (Appendixes 6 and 7).

No data suggests that skull ornamentation (character 1) necessarily have to develop a grooved pattern (state 1) before showing a pitted pattern (state 2). The same applies to the general morphology of the rostrum (character 3), as platyrostral forms (state 3) may develop into broad oreinrostral (state 1) or nearly tubular forms (state 2), and forms with nearly tubular rostrum may develop from narrow oreinrostral (state 0) or platyrostral forms. The size and number of palpebrals (character 65) is poorly known for taphonomic reasons, as these elements can be easily lost in the burial process, and the ordering can only introduce an additional bias. The development of an antorbital fenestra (character 67) may be recognizable as few discrete states, but the difference between states 1-3 do not necessarily need to be linear. Apart from that, minor differences on the size of the fenestrae may be an artifact of preservation. Multistate characters referring to repetitive structures (*e.g.* vertebrae, teeth) should not be subject to ordering because the number of elements can be the result of deletions and additions in any point of the series (characters 105 and 107). The position of the ascending jugal process (=postorbital jugal process; character 143), which takes part in the postorbital bar, may be the result of the postorbital bar inclination or either the development/ shortening of the anterior or the posterior process, which hinders the ordering of states.

Characters excluded in the second step are mostly related to dentition, and are subject to a series of problems. Characters 105-107 referred to the number of teeth of the premaxilla and maxilla. Although widely used (*e.g.*, Wu & Sues, 1996; Ortega *et al.*, 2000; Pol & Apesteguia, 2005; Zaher *et al.*, 2006), the number of teeth for a single element may not represent true homologous conditions. In fossil crocodylians, the reduction of the dental series can be the result of loss of anterior, middle or posterior elements, as in the case of number of vertebrae. Furthermore, the existence of an intermediate tooth in the upper series complicates interpretation and coding. The information was reintroduced as characters 200-202, considering the position of this intermediate tooth and the exclusive premaxillary and maxillary series as independent characters. Nevertheless, this set of characters is still not free from criticism, as it ignores changes in size and morphology throughout the series. Character 120, as originally published (Ortega *et al.*, 2000) refers to the presence of a carina in teeth. In fact, as explored by Prasad & Broin (2002), Andrade (2005) and Andrade & Bertini (2005b), carinae show variation in morphology and distribution over the dental series, and two different situations are recognized here. The true ziphodont type of carina is present in anterior teeth of highly predaceous forms, and can also develop on posterior teeth. An alternate situation is present in other species, where carinae are completely absent from anterior teeth, but are present in posterior teeth and show a different morphology of denticles, possibly related to processing food. The information was reintroduced as character 204. Character 194 dealt on the presence of procumbent alveoli in the anterior dentition, thus avoiding morphological differences of teeth related to those alveoli. Procumbent dentition is probably related to functional aspects of feeding, but may have evolved multiple times from quite different conditions. In fact, the original coding ignores that, in most eusuchians (*e.g.*, *Gavialis*, *Crocodylus*) and several Mesoeucrocodylia, the alveoli are usually inclined anteriorly and teeth are procumbent, both in the mandible and in the premaxilla. This may not be so evident, as these teeth are often strongly curved caniniforms, and the apex is directed to the occluding plane rather than anteriorly. The alveoli and teeth, nonetheless, are inclined anteriorly. The information is reintroduced with character 205, with reference to dental morphology. Nevertheless, it should be stressed that the new coding still does not solve the problem of adequately representing this information, as inclined alveoli can occur in different sections of the jaws. Furthermore, deformation may easily introduce bias in the coding of this character.

Character not comprising the dentition relate to the jugal, lachrymal and maxilla. The contact between jugal and lachrymal (character 192) is usually present in Mesoeucrocodylia, excluding the maxilla from the orbit. The maxillary participation to the orbit was already pointed out by ANDRADE (2005; character 16) and is also present in *Malawisuchus* and *Uruguaysuchus*. As in MARTINELLI (2003) and ANDRADE (2005), the maxilla of *Comahuesuchus* does not take part of the orbit (*contra* ZAHER *et al.*, 2006). The information was reintroduced with character 203. Character 193, the presence of an anteriorly directed enlarged neurovascular foramen on the jugal anterior ramus of some notosuchians (*Mariliasuchus*, *Comahuesuchus* and *Sphagesaurus*), was previously introduced by ANDRADE (2005; character 43). Furthermore, ANDRADE (2005) includes a third state covering the existence of small ventrally directed foramina (generally four) close to the contact with the maxilla, present in eusuchians. The information was reintroduced as character 199.

RESULTS

PRELIMINARY ANALYSIS

Only a single most parsimonious tree was obtained from the preliminary analysis (Fig.16; Length = 468, CI = 0.4829, RI = 0.6372, RC = 0.3077, HI = 0.5171). The topology shows a well supported closest relationship between *Mariliasuchus* and *Notosuchus* (bootstrap = 85%; branch decay = 4), as proposed originally by CARVALHO & BERTINI (1999) and consistent with Notosuchidae. *Sphagesaurus huenei* also shows a close relationship, in a well supported unnamed clade including Notosuchidae (bootstrap = 82%; branch decay = 5). *Comahuesuchus* and *Chimaerasuchus* are successively more distant sister-groups, but lacking a good support (bootstrap < 60%; branch decay = 1). A larger group including these species and the Baurusuchidae shown to be only slightly better supported (bootstrap < 50%; branch decay = 2).

Candidodon lays as sister-clade of *Uruguaysuchus*, as part of a more basal notosuchian lineage (along with *Simosuchus* and *Malawisuchus*). The support for this group is poor (bootstrap < 50%; branch decay d•2). Nevertheless, the close relationship between *Candidodon* and *Mariliasuchus*, proposed by CARVALHO *et al.* (2004), is extensively rejected. Partial corroboration of main aspects of this analysis is provided by further analysis based on ZAHER *et al.* (2006). Furthermore, a few other aspects deserve attention. Notosuchia (*sensu* SERENO *et al.*, 2001) finds a strong support (bootstrap = 79%; branch decay = 5), but does not include *Anatosuchus* or *Araripesuchus*. Furthermore, these taxa are represented as related to the neosuchian lineage, a position reasonably well supported in both cases (bootstrap = 55%; branch decay = 3). The close relationship between *Comahuesuchus* and *Anatosuchus*, proposed by SERENO *et al.* (2003), is extensively rejected. *Sebecus* appear as the sister group of Eusuchia, a relationship that finds a strong support (bootstrap = 79%; branch decay = 5). Although there is a lack of other highly predatorial mesoeucrocodylian taxa within the analysis (*e.g.*, *Libycosuchus*, *Bergisuchus*, *Bretesuchus*, *Hamadasuchus*, *Pabweshi*), the results do not support Sebecosuchia or Ziphosuchia.

SECOND ANALYSIS

THE PRELIMINARY ANALYSIS OF ZAHER *ET AL.* (2006) – Considering only the original matrix (with exclusion of character 5), the ordered analysis is more resolved than the unordered analysis (96 MPTs, 619 steps). The unordered analysis with the same dataset solves the relationship between *Notosuchus* and the other notosuchians, although leads to a poor resolution for Neosuchia (*sensu* SERENO *et al.*, 2001).

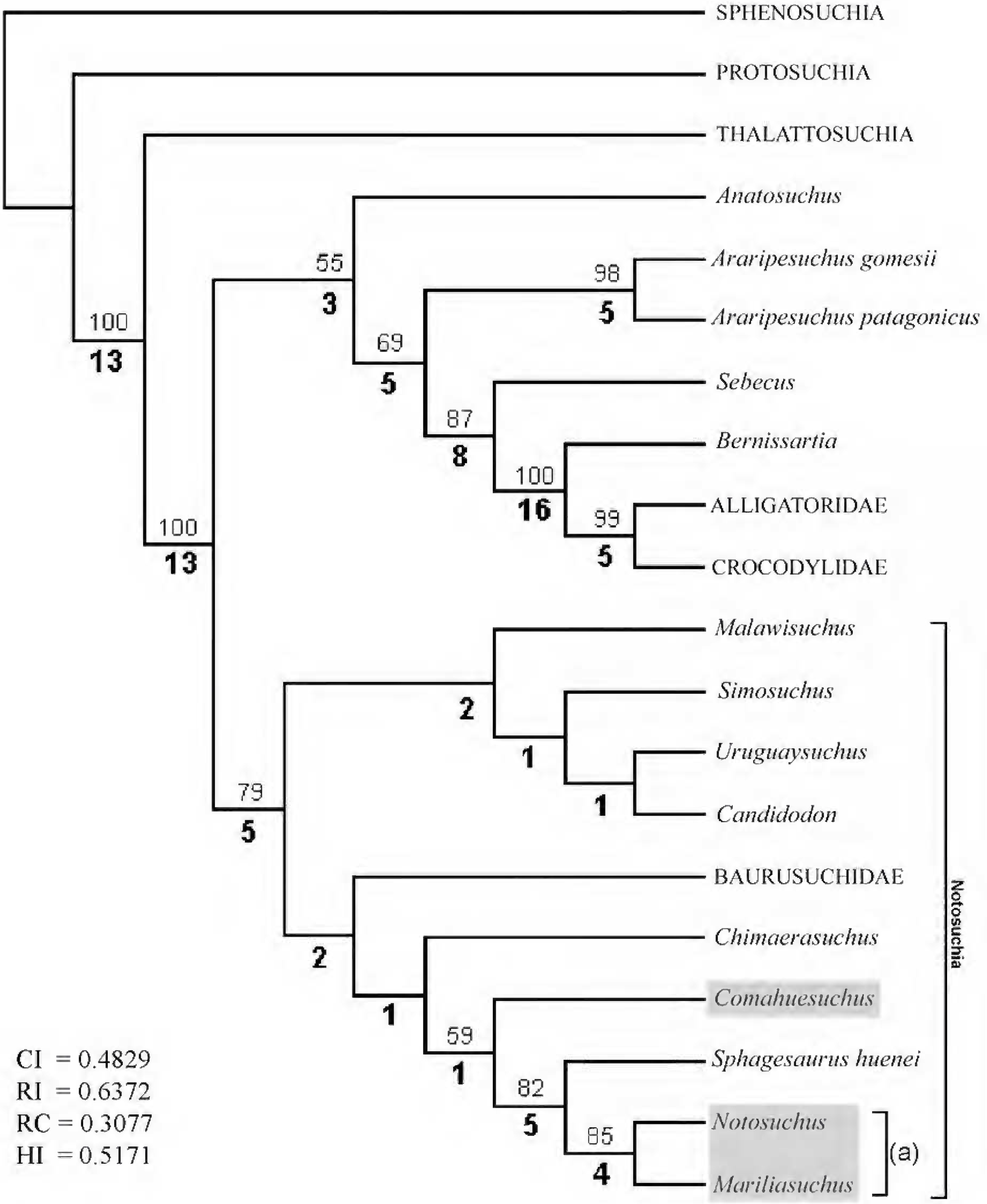

Fig.16- Single most parsimonious tree (468 steps) based on dataset by Andrade (2005), showing the position of Notosuchidae (a) within Notosuchia (*sensu* Sereno *et al.*, 2001). Support indicated for each node, showing bootstrap for values over 50% and branch decay (bold numbers) indexes. Note the position of *Notosuchus* in relation to *Mariliasuchus* and *Comahuesuchus*, indicated by the shaded areas, and the distant relationship with *Candidodon* and *Malawisuchus*.

In this analysis, *Notosuchus* remained as a sister-clade to *Mariliasuchus*+*Comahuesuchus*. Successive weighting of the unordered data confirms this relationship, with a slight increase of resolution inside Neosuchia.

First step of the second analysis – The result obtained from step one (Fig.17), where morphological information was corrected, solved the position of *Notosuchus* as sister-clade of *Mariliasuchus*+*Comahuesuchus*. In the strict consensus (95 MPTs, 615 steps), several polytomies are present (as in the unordered analysis of the original dataset). Ordering (22 MPTs, 629 steps) only improves the position of *Gavialis* and *Eutretauranosuchus*, while successive weighting enhances the resolution of basal neosuchian longirostrine forms (Teleosauridae, Dyrosauridae+*Sokotosuchus*). In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms. *Candidodon* remains as sister-group to *Malawisuchus*, as in the original analysis, but *Simosuchus* appears as part of this lineage. *Uruguaysuchus* appears as a separated, more basal lineage within Notosuchia. *Araripesuchus* is shown as the basalmost group of Notosuchia (*sensu* Sereno *et al.*, 2001). The position of *Hylaeochampsa* remains unresolved relative to *Borealosuchus* and the extant crocodylians.

The result of this analysis shows that the information corrected is crucial to avoid incongruences that affect the position of *Notosuchus*. Ordering is an important element to improve resolution within Neosuchia, but successive weighting introduces more resolution, for this particular dataset.

Second step of the second analysis – Step two verified the possible biased effect of a limited number of characters, by means of their exclusion. The unordered analysis (Fig.18) shows a similar strict consensus (76 MPTs, 583 steps) to the previous step, except for two noticeable changes: (i) an improvement in the relationships within Neosuchia; (ii) a shift in position between *Comahuesuchus* and *Notosuchus*, the later of which is then shown as sister-clade to *Mariliasuchus*. Ordered analysis (25 MPTs, 597 steps) and successive weighting do not change either the *Notosuchus*+*Mariliasuchus* exclusive relationship or the position of *Comahuesuchus*, but further improves resolution inside Neosuchia. In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms. *Candidodon* appears as sister-group to *Malawisuchus*+*Simosuchus*. *Uruguaysuchus* remains as a separated, more basal lineage within Notosuchia. *Araripesuchus* figures as the basalmost group of Notosuchia. Also in all cases, *Hylaeochampsa* remains unresolved and atoposaurids maintained a closer position to *Alligator* than to the basal neosuchian longirostrine forms.

The result of this analysis shows that the removed characters were essential in establishing a link between *Mariliasuchus* and *Comahuesuchus*. This link is not supported otherwise, but the result provides no answer to which factor could determine this relationship. It could be either the lack of the excluded information *per se* or the construction of characters and definition of states. This problem was addressed in the last step of the analysis. The exclusion of these characters did not change the results in Neosuchia, or the effect of ordering and successive weighting. Ordering is again an important element to improve resolution within Neosuchia, but successive weighting introduces more resolution.

Third step of the second analysis – In this step the information previously excluded is reintroduced with the addition of seven characters. Unordered analysis (225 MPTs, 621 steps) shows six polytomic groups (Fig.19), only two of them in Notosuchia. In the notosuchian lineage, the *Mariliasuchus*+*Notosuchus* clade is also present, but *Comahuesuchus* occupies an even more basal position than in the previous step. *Simosuchus* shows a shifting behavior and induces a polytomy with the closest taxa. The reintroduction of the information did not affect the relationships inside Neosuchia. Bootstrap shows a reasonable support (>50%) for approximately 50% of the mesoeucrocodylians, but only eight clades (approximately 30%) show a good support index (≥75%). Ordering (45 MPTs, 635 steps) only improves the position of *Gavialis* and *Eutretauranosuchus*. Successive weighting affects the longirostrine forms, as in the previous steps, but also *Comahuesuchus* and *Simosuchus*, from the notosuchian branch.

In all cases, *Sphagesaurus* figures as sister-group to *Chimaerasuchus*, representing a lineage associated to *Baurusuchus* and similar forms.

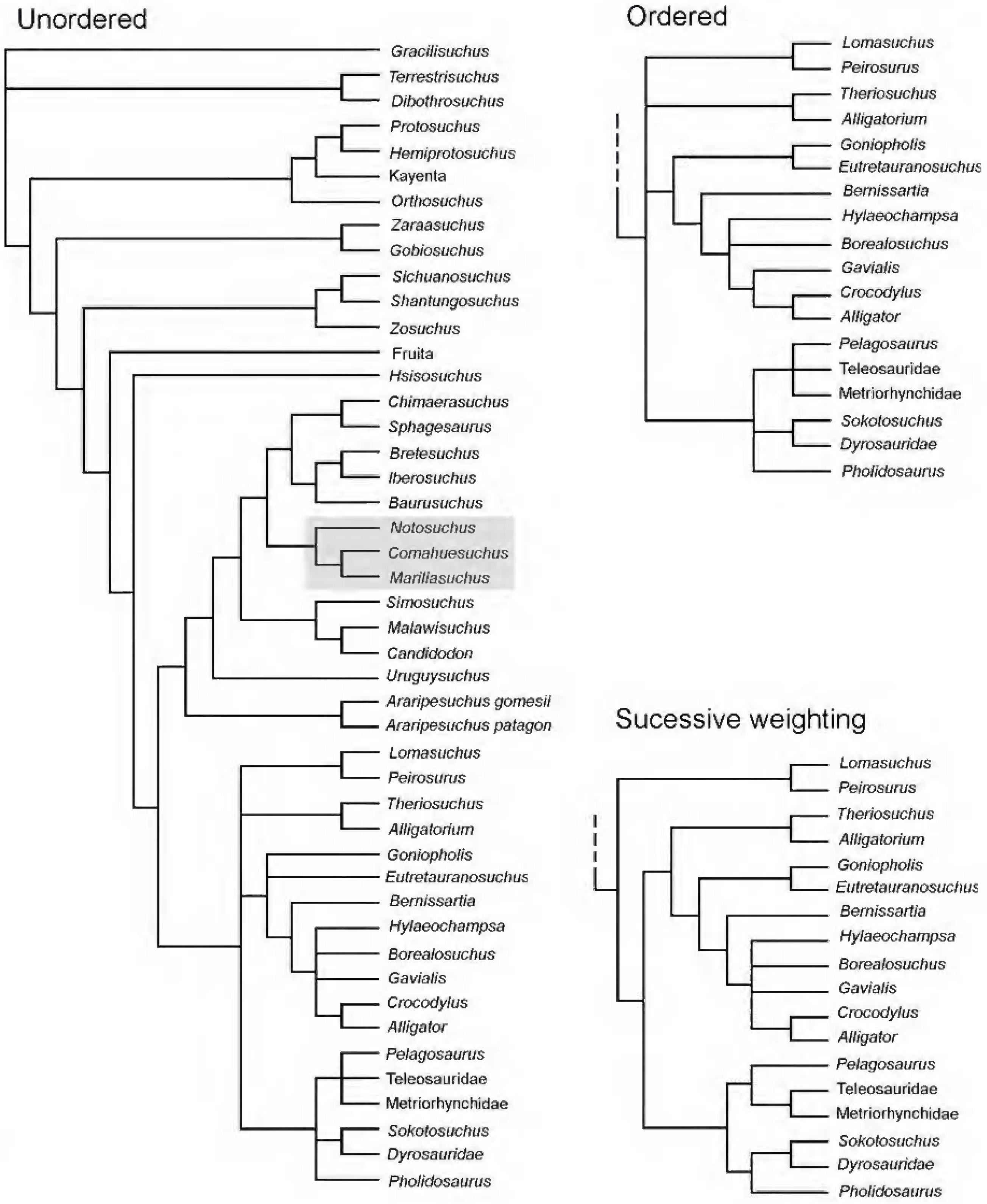

Fig.17- First step in the revaluation of the original dataset by Zaher *et al.* (2006), with corrected data from the matrix. Unordered analysis led to a strict consensus of 95 MPTs (615 steps, CI = 0.43). Ordered analysis (22 MPTs, 629 steps) and successive weighting (right) introduced changes only to the neosuchian branch. Wagner parsimony applied for 18 characters. Note the stable position of *Notosuchus* relative to *Comahuesuchus* and *Mariliasuchus*, indicated by the shaded area, and the distant relationship with *Candidodon* and *Malawisuchus*.

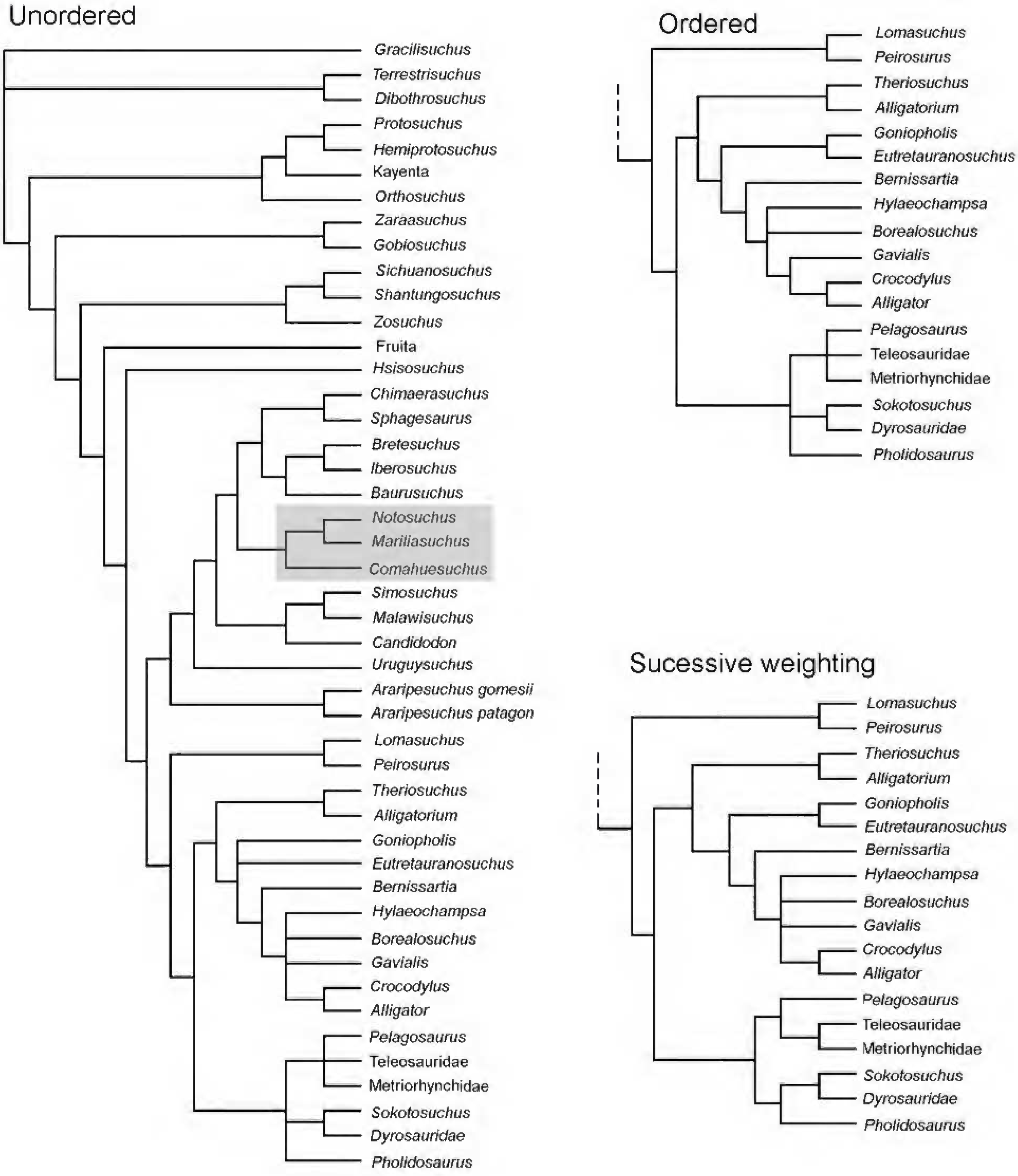

Fig.18- Second step in the revaluation of the original dataset by Zaher *et al.* (2006), with the exclusion of problematic characters (5, 105, 107, 120, 192, 193, 194). The unordered analysis led to a strict consensus of 76 MPTs (615 steps, CI = 0.43). Ordered analysis (25 MPTs, 597 steps) and successive weighting (right) only affected the neosuchian branch. Wagner parsimony applied for 18 characters. Note the shift in the position of *Comahuesuchus* and *Mariliasuchus* relative to *Notosuchus* (shaded area), showing the effect produced by the exclusion of characters.

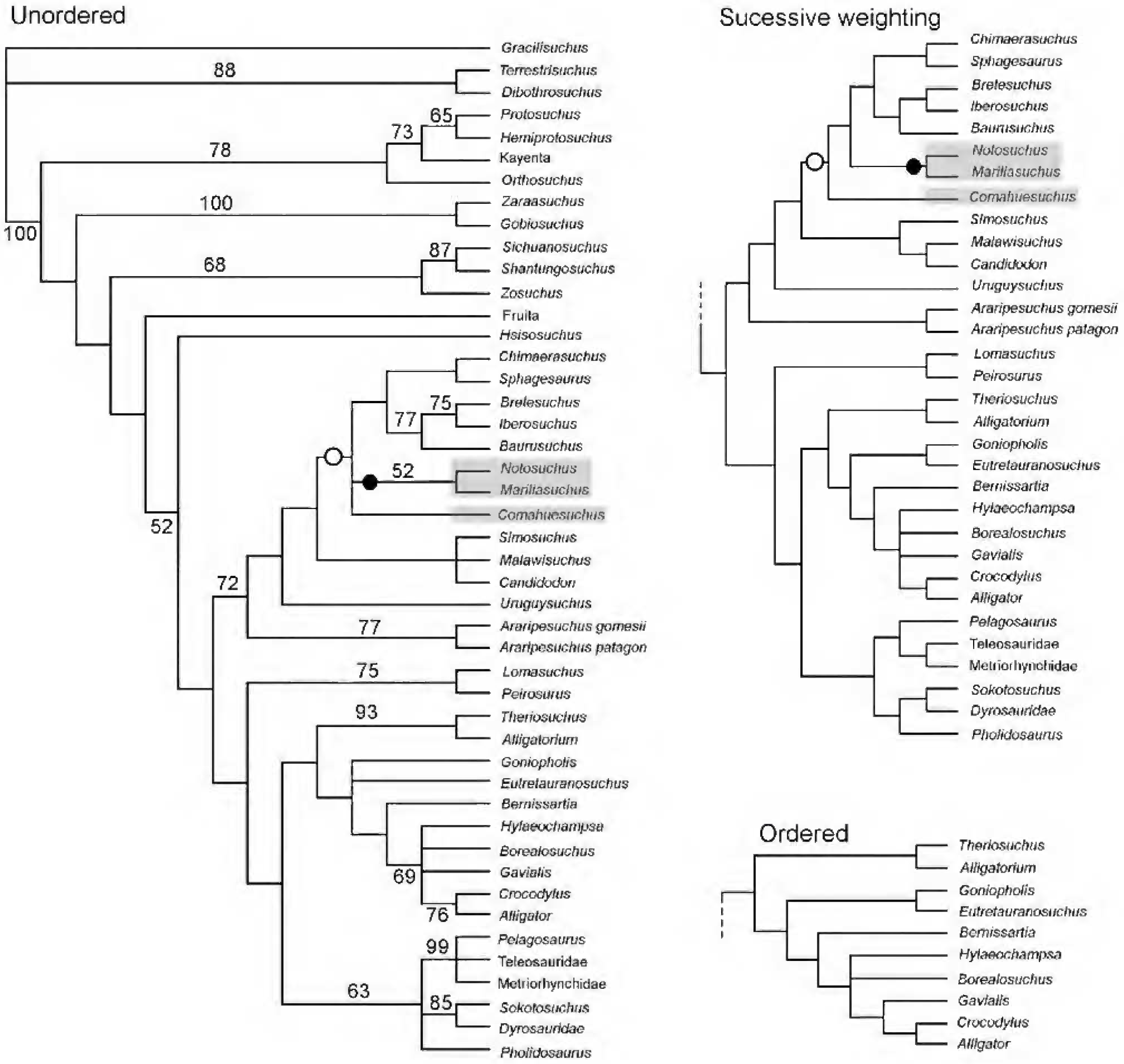

Fig.19- Third step in the revaluation of the original dataset by Zaher *et al.* (2006), with the reintroduction of the information excluded in the previous step, using reorganized characters. The positions of *Notosuchus*, *Mariliasuchus* and *Comahuesuchus* are indicated by a shaded area. The unordered analysis (left) led to a strict consensus of 225 MPTs (621 steps, CI = 0.43, RI = 0.68, RC = 0.29), where *Comahuesuchus* shows a shifting behavior, either figuring as sister-clade to Notosuchidae (black circle) or to all other derived notosuchians (white circle). Ordered analysis (bottom right) (45 MPTs, 635 steps) only affected the neosuchian branch, but the use of successive weighting (top right) affects Notosuchia and determines an even more basal position for *Comahuesuchus*. Numbers on each node refer to bootstrap. Ordered option applied for 19 characters. Note the position and reasonable support for *Mariliasuchus* and *Notosuchus*, but the overall poor support for most relations within Mesoeucrocodylia.

Candidodon, *Malawisuchus* and *Simosuchus* appear as a single lineage of notosuchians. *Uruguaysuchus* appears as a separated, more basal lineage within Notosuchia. *Araripesuchus* figures as the basalmost group of Notosuchia (*sensu* SERENO *et al.*, 2001). Also in all cases, the position of *Hylaeochampsa* remains unresolved relative to *Borealosuchus* and the extant eusuchians, and atoposaurids mantained a closer position to *Alligator* than to the longirostrine forms.

The reintroduction of these characters did not change the results in Neosuchia, as the use of ordering and successive weighting. Nevertheless, the reintroduction of information clearly affects the position of *Comahuesuchus* and improves the influence of successive weighting over *Comahuesuchus* and *Simosuchus*. In the unordered and ordered topologies, *Comahuesuchus* has collapsed into a position as basal as the lineage that leads to *Sphagesaurus* and the highly predaceous notosuchians (*e.g.*, Baurusuchidae). When successive weighting was applied to improve resolution, *Comahuesuchus* assumes an even more basal position (with a similar effect to the position of *Simosuchus*). Once more, successive weighting also introduces more resolution than ordering, for this particular dataset.

OVERALL RESULTS OF THE SECOND ANALYSIS – The second analysis was introduced to corroborate results from the preliminary analysis with an independent dataset. Furthermore, it allows understanding the effect that characters, information and options had over the final topology. The results from the second analysis show that: (i) corrected information was determinant to define the position of *Notosuchus*; (ii) the exclusion of the selected characters clearly has an effect on the position of *Comahuesuchus*; (iii) the reintroduction of the information does not support a closest relationship between *Comahuesuchus* and *Mariliasuchus*; (iv) in no single result, *Candidodon* shows a close relationship with *Mariliasuchus*; (v) successive weighting and ordering produce essentially concordant results, but successive weighting introduces more resolution in this particular dataset. In overview, the implementation of the third step shows that the construction of a small group of characters may be determinant to the position of certain terminals within an analysis. In this special case, *Comahuesuchus* is particularly affected (but not *Notosuchus*). It was the particular way the selected characters are constructed that led to changes to the position of *Comahuesuchus*. On the other hand, correction of the morphologic information in step one was determinant to improve the position of *Notosuchus*.

The combined results from the preliminary and the second analysis show that: (i) *Mariliasuchus* and *Notosuchus* are closely related forms; (ii) the position of *Comahuesuchus* is poorly defined, but it may be closely related to *Notosuchus*+ *Mariliasuchus* than to any other notosuchian; (iii) a closer exclusive relationship between *Candidodon* and *Mariliasuchus* is extensively rejected; (iv) *Mariliasuchus, Notosuchus, Comahuesuchus, Sphagesaurus, Chimaerasuchus* and highly predaceous notosuchians seems to be closely related to each other than to any other notosuchian; (vi) *Candidodon, Malawisuchus* and *Simosuchus* possibly constitute a different notosuchian lineage, which may include *Uruguaysuchus*; (v) there is an overall poor support for most clades within Notosuchia and Neosuchia, especially for basal branches within these groups.

DISCUSSION

The comparison between *Notosuchus, Mariliasuchus, Comahuesuchus* and *Candidodon* allowed the identification of morpho-anatomical similarities and discrepancies between these taxa. Neither the jugal foramen, nor the absence of contact between lachrymal and jugal are exclusive characteristics of *Mariliasuchus* and *Comahuesuchus*. There are further similarities regarding the dentition that are often ignored because of a lack of agreement on the morphology, either for *Notosuchus* and *Mariliasuchus*. The intermediate position occupied by the first postcaniniform is problematic, as it is difficult to recognize which element (the premaxilla or the maxilla) is actually related to the tooth. On the other hand, the fact that both the premaxilla and the maxilla take part on the first postcaniniform alveolus represents an important observation. Other aspects include the development of fenestrae. Though *Mariliasuchus* and *Comahuesuchus* do not have an antorbital fenestra, unlike *Notosuchus*, this condition is also present in other closely related forms (*Sphagesaurus huenei, Chimaerasuchus*?, baurusuchids). On the other hand, *Mariliasuchus* and *Notosuchus* are the only notosuchians that have maxillo-palatine fenestra, which show exactly the same morphology. The morpho-anatomical study shows that there is a lack of important information on *Comahuesuchus* and *Candidodon*, due to the incompleteness of the specimens, although critical information on *Candidodon* only awaits description. The morpho-anatomical study also confirmed the autapomorphic features of *Notosuchus*, *Mariliasuchus* and *Comahuesuchus* previously described by several authors (WOODWARD, 1896; GASPARINI, 1971; BONAPARTE, 1991; CARVALHO & BERTINI, 1999; MARTINELLI, 2003; ANDRADE, 2005; ZAHER *et al.*, 2006).

Intra-specific variability still does not play an important role in phylogenetic analysis, because there is lack of data for most species. Even for *Notosuchus* and *Mariliasuchus*, there is only a limited amount of information that can be used. Both species show intra-specific variability regarding the parietal morphology, which may be linked to sexual dimorphism, but this depends on the proper study of larger numbers of specimens. At least for *Notosuchus*, the different types of parietal seem to occur in a bimodal distribution within the sample. However, it is currently impossible to evaluate the occurrence of sexual variability in other notosuchian taxa due to the small samples currently available. Ontogenetic variability may be more clearly identified in *Mariliasuchus*, but several important aspects need evaluation (*e.g.*, rotation of teeth, rostrum differentiation, development of ornamentation). As for the sexual dimorphism, the sample does not allow identification of ontogenetic variability in most other Mesoeucrocodylia.

Notosuchus and *Mariliasuchus* show a great degree of resemblance that led to the reevaluation of their phylogenetic relationships, confirming their proximity, as originally proposed by CARVALHO & BERTINI (1999). Therefore, *Mariliasuchus* should be understood as a Notosuchidae, rather than a Candidodontidae or a Comahuesuchidae. The comparative study and the phylogenetic analysis do not disprove ZAHER *et al.* (2006), but in fact supports the recognition of similarities of *Comahuesuchus* and Notosuchidae. Most of all, results presented here show that the position of *Comahuesuchus* lacks stability, rather than the position of *Notosuchus*.

In overview, much still needs to be done to improve the understanding of crocodylomorph evolution. Several taxa still present a reasonable amount of missing data. As in the character list presented here (Appendix 2), the main part of data from most analysis focus on cranial characters (82.5%, in the case of the preliminary analysis). Even considering the current information on postcranial material, the amount of missing data is extensive. The relevance of postcranial remains for phylogenetic analysis has already been pointed out by POL (1999, 2005). Even though postcranial remains are reported for several taxa, the material is still unpublished (*e.g.*, *Mariliasuchus, Baurusuchus, Uberabasuchus*). The extensive use of characters related to acquisition of food (rostrum, mandible, dentition) may be one of the factor introducing misleading information and leading to incongruent homoplastic datasets. The detailed revision of the character-states and recognition of specific conditions may help to reduce the number of homoplastic conditions throughout the analysis, increasing support and stability.

As a result of the highly homoplastic datasets and poor support and stability, the current bibliography provides a number of alternative hypothesis for the evolution of mesoeucrocodylians (*e.g.*, BENTON & CLARK, 1988; CLARK, 1994; WU & SUES, 1996; GOMANI, 1997; BUCKLEY *et al.*, 2000; ORTEGA *et al.*, 2000; SERENO *et al.*, 2001, 2003; MARTINELLI, 2003; POL, 2003; POL & NORELL, 2004a, 2004b; POL & APESTEGUIA, 2005; ANDRADE, 2005; FIORELLI, 2005; TURNER & CALVO, 2005; TURNER, 2006; ZAHER *et al.*, 2006; LARSSON & SUES, 2007; LAUPRASET *et al.*, 2007). Nevertheless, in a general overview, most aspects from the preliminary analysis presented here still reach some measure of agreement with other analysis. In particular, comparison was made to another dataset to falsify the results in respect to the phylogenetic position of *Mariliasuchus*.

Both analysis indicate that *Notosuchus* is closely related to *Mariliasuchus*. When potentially misleading data (due to character construction and coding) was excluded from the second analysis, no evidence of an exclusive relationship between *Mariliasuchus* and *Comahuesuchus* remained. When data on dentition and jugal were treated on the same manner in both analysis, results pointed to an exclusive monophyletic clade joining *Mariliasuchus* and *Notosuchus*, with a rather more basal position to *Comahuesuchus*. In similar conditions, both datasets performed in the same manner, indicating that interpretation of the morphology and construction of characters are the true determining agents on the position of these taxa. On the other hand, the inclusion of new cranial data from NOBRE & CARVALHO (2002) and changes to the character list did not influence the position of *Candidodon*. In fact, all analysis show that *Candidodon* seems to be associated with *Malawisuchus* (as originally proposed by NOBRE & CARVALHO, 2002), rather than to *Mariliasuchus*.

In overview, apart from the limited shifting behavior shown by some of the taxa, the structure is the same. *Notosuchus* and *Mariliasuchus* are closely related, and this group is related to highly predaceous notosuchians (*Baurusuchus*, *Bretesuchus*, *Iberosuchus*), as to the clade *Sphagesaurus*+ *Chimaerasuchus*. Other notosuchians, such as *Candidodon, Malawisuchus* and *Uruguaysuchus*, seem to be in a reasonably stable position, much more basal.

The preliminary analysis also rejected the sister-group relationship between *Anatosuchus* and *Comahuesuchus*, originally proposed by Sereno *et al.* (2003) and followed by Turner & Calvo (2005) and Turner (2006). Such relationship has been repeatedly repelled by other works (Martinelli, 2003; Andrade, 2005; Andrade *et al.*, 2006; Zaher *et al.*, 2006), but the problem still deserves further clarification. Nevertheless, they seem to represent different patterns of skull construction and eventual rostral similarities are more likely to be convergences, rather than secondary homologies. These convergences can be explained by common aspects of their paleoecology (*e.g.*, composition of diet, foraging mode). The genus *Araripesuchus*, due to its shifting position in different analysis, may either be considered as a basal Neosuchia (according to the definitions by Sereno *et al.*, 2001), as previous analysis already suggested (*e.g.*, Buckley *et al.*, 2000; Ortega *et al.*, 2000; Pol, 2003; Pol & Apesteguia, 2005; Turner & Calvo, 2005; Turner, 2006; Lauprasert *et al.*, 2007) or a basal Notosuchia (Fiorelli, 2005; Fiorelli & Calvo, 2005; Zaher *et al.*, 2006). The future recognition of undisputable characters uniting *Araripesuchus* and notosuchians may contribute to the debate. A better approach could be the recognition of the genus as an independent lineage, which may either be related to Neosuchia (*sensu* Benton & Clark, 1988) or to Notosuchia (*sensu* Gasparini, 1971). Here, the use of linnean nomenclature becomes more adequate than the "phylogenetic" definition, since in the last there is no clear content of these clades. Currently, the traditional linnean definition of Notosuchia may appear as paraphyletic due to inclusion of *Araripesuchus* and exclusion of *Baurusuchus* and related forms. The exclusion of taxa with unstable behavior (*Araripesuchus, Anatosuchus*) and inclusion of baurusuchids (and relater forms) will allow a wider and more straightforward use of the linnean definition of Notosuchia. On the other hand, this redefinition does mean that the *Araripesuchus* and the notosuchian lineages are not related, but only that *Araripesuchus* is not a Notosuchia. This definition would be in agreement with most published phylogenetic works (*e.g.*, Benton & Clark, 1988; Clark, 1994; Buckley *et al.*, 2000; Ortega *et al.*, 2000; Pol, 2003; Pol & Apesteguia, 2005; Turner & Calvo, 2005; Turner, 2006; Zaher *et al.*, 2006; Lauprasert *et al.*, 2007).

Further problems remain to be solved also in the notosuchian branch. *Comahuesuchus* and *Simosuchus* seem to show a particularly important unstable behavior. Their shifts in the apical and the basal sections of the topologies may account for the low branch decay and bootstrap indexes present in the notosuchian branch of the preliminary analysis. Despite what has been done to describe these species, there is still much to be understood about them. *Comahuesuchus* would benefit from a greater number of more complete specimens, as well as information on teeth. On the other hand, fossil crocodylians long described (*Uruguaysuchus, Candidodon*) need an extensive reevaluation, which would certainly bring further details into the analysis, help to stabilize the position of the shifting taxa and eventually correct misled interpretations.

CONCLUSIONS

Notosuchus and *Mariliasuchus* are closely related notosuchians, sharing several similar characteristics (*e.g.*, teeth, premaxilla, maxillo-palatine fenestrae, choanae, quadrate fenestrae, retroarticular process). Similarities between dentition may indicate similar foraging behaviour, and variability in the parietal morphology may indicate sexual dimorphism in both taxa. *Notosuchus* and *Mariliasuchus* come from the Upper Cretaceous of South America, from units interpreted as semi-arid environments and areas not very distant from each other. The idea that either *Notosuchus* or *Mariliasuchus* may be related to the Lower Cretaceous *Candidodon* is unlikely, given the phylogenetic results obtained. Nevertheless, data presented and discussed here support that both *Notosuchus* and *Mariliasuchus* may show a close relationship with *Comahuesuchus*, which is also from the Upper Cretaceous of South America. In a broader view, *Comahuesuchus*, *Mariliasuchus* and *Notosuchus* certainly show to be more closely related to each other than to *Malawisuchus*, *Candidodon*, *Uruguaysuchus* or even with *Anatosuchus* and *Araripesuchus*. *Araripesuchus* and *Anatosuchus* may be better defined as independent lineages, although the position of *Anatosuchus* still needs further clarification.

They may either be related to Neosuchia (*sensu* Benton & Clark, 1988) or to Notosuchia (*sensu* Gasparini, 1971), but there is no need to consider them as part of these groups in a linnean definition.

In a broad view, there are still several disagreement points in the current phylogenetic hypothesis for evolutionary relationships of Mesoeucrocodylia. Most frameworks do not agree in many aspects, presenting an overall poor support. A few of these works may be affected by a biased sample of taxa and even by problems on the construction of characters. The overall structure of the group, as the internal structure of Notosuchia (*sensu* Sereno *et al.*, 2001) is yet to be refined. A more comprehensive idea on the evolution of notosuchians and mesoeucrocodylians will only be achieved with detailed comparative description of specimens, reduction of missing data currently in the analysis, evaluation of intraspecific variability in range and further discussion on character construction and recognition of independent states.

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APPENDIX 1

Specimens of *Notosuchus*, *Mariliasuchus* and other Notosuchia (*sensu* Gasparini, 1971) examined. Type specimens in bold. The number in parentheses is the original designation for MLP specimens of *Notosuchus*, given by A. Smith Woodward. *Notosuchus* lectotype elected by Gasparini (1971), from the original assemblage of specimens used in the original description (Woodward, 1896).

Araripesuchus patagonicus – MUCPv-267, MUCPv-268, MUCPv-268b, **MUCPv-269**, MUCPv-270.

Candidodon itapecuruense – UFRJ-DG-113-R, UFRJ-DG-114-R.

Comahuesuchus brachybuccalis – MACN-Pv-N-31, MOZ-P-6131, **MUCPv-202**.

Mariliasuchus amarali – MN 6298-V, MN 6756-V, **UFRJ-DG-50-R**, UFRJ-DG-105-R, UFRJ-DG-106-R, URC R•67, URC R•68, URC R•69, URC R•74 and URC R•75.

Notosuchus terrestris – MACN–Pv–N–22, MACN–Pv–N–23, MACN–Pv–N–24, MACN–Pv–N–43, MACN–Pv–N–107, MACN–Pv–RN–1015, MACN–Pv–RN–1037, MACN–Pv–RN–1038, MACN–Pv–RN–1039, MACN–Pv–RN–1040, MACN–Pv–RN–1041, MACN–Pv–RN–1043, MACN–Pv–RN–1044, MACN–Pv–RN–1045, MACN–Pv–RN–1046, MACN–Pv–RN–1047, MACN–Pv–RN–1048, MACN–Pv–RN–1118, MACN–Pv–RN–1119, MLP–64–IV–16–1, **MLP–64–IV–16–5(253)**, MLP–64–IV–16–6(203), MLP–64–IV–16–7(219), MLP–64–IV–16–8(209), MLP–64–IV–16–10(221), MLP–64–IV–16–11, MLP–64–IV–16–12, MLP–64–IV–16–13, MLP–64–IV–16–14, MLP–64–IV–16–15, MLP–64–IV–16–16, MLP–64–IV–16–17, MLP–64–IV–16–18, MLP–64–IV–16–20, MLP–64–IV–16–21, MLP–64–IV–16–22, MLP–64–IV–16–23, MLP–64–IV–16–24, MLP–64–IV–16–25, MLP–64–IV–16–28, MLP–64–IV–16–30, MLP–64–IV–16–31(206), MPCA–Pv–528; MPCA–Pv–789/1; MPCA–Pv–791.

Sphagesaurus huenei – **DGM-332-R**, DGM-333-R, DGM-1411-R, RCL-100.

APPENDIX 2

List of characters used in the phylogenetic analysis. Total number of characters 183, distributed as follows: 120 cranial (65.57%); 28 dental (15.3%); 32 postcranial (17.5%). Main anatomical element indicated in bolt, in the description of the character. Characters either new or obtained from previous works, designated by code and original number, presented in chronological order inside brackets. 'm' indicates characters modified from the original. Codes for bibliographic origin of characters as follows: A = Andrade, 2005; Buckley *et al.*, 2000; C = Clark, 1994; G = Gomani, 1997; M = Martinelli, 2003; O = Ortega *et al.*, 2000; Pa = Pol, 1999; Pb = Pol, 2003; S = Sereno *et al.*, 2003; W = Wu & Sues, 1996.

General (3 characters; 1.64% of total)

1. ***Skull surface*** *[O01]*: **(0)** smooth or ornamented with an irregular pattern of ridges rugosities and anastomosing grooves; **(1)** ornamented with circular to polygonal pits, with eventual sulcation (not anastomosed).
2. ***Skull height****, in posterior view [C03m; S06m; P03m; A02]*: **(0)** skull higher than wider or subequal; **(1)** skull larger than higher.
3. *Orientation of the* ***orbits*** *[A3]*: **(0)** lateral; **(1)** laterodorsal.

Rostrum (28 characters; 15.3% of total)

4. *Proportional length of the* ***rostrum*** *in lateral view [W4m]*: **(0)** short, orbits at the skull midlength; **(1)** long, orbits at the posterior half of the skull.
5. ***Rostrum*** *height, anterior view [C03]*: **(0)** rostrum higher than wider; **(1)** rostrum subquadrate; **(2)** rostrum wider than higher.
6. ***Rostrum****, in dorsal view [C02]*: **(0)** is narrow, abruptly widening to adjust the skull outline; **(1)** gradually fits the skull outline, with a general triangular shape.
7. *External* ***nares*** *[C06; S02m+07m; Pb06m]*: **(0)** terminal, opening anteriorly; **(1)** lateral or semi–lateral; **(2)** anterodorsal or dorsal.
8. ***Internarial bar*** *[S7]*: **(0)** absent; **(1)** gracile, narrow; **(2)** present as a wide bar.
9. ***Anterorbital region*** *[C68m; W16m; S03m]*: **(0)** smooth and flat; **(1)** vestigial or small antorbital fenestra; **(2)** well developed antorbital fenestra.
10. *Anteriormost portion of the* ***premaxilla****, at the region at the front and below the narial opening [C5; S9]*:

(0) narrower than the lateral part of the premaxilla; **(1)** high, subequal to the height of the lateral part of the premaxilla.

11.***Premaxilla–maxilla foramen*** *[Pa149; O13; Pb135]*: **(0)** absent; **(1)** present.

12.***Premaxilla–maxilla suture****, lateral view [A13m]*: **(0)** straight, vertical; **(1)** curved or composed by two planes (lower vertical, upper diagonal), with a posterodorsal process, flanking the nasals; **(2)** straight, diagonal.

13.*Inferior border of the* ***premaxilla–maxilla suture****, in lateral view [C09m]*: **(0)** without constriction or notch, region between premaxilla and maxilla flat, composing a straight border; **(1)** evident constriction, forming a notch.

14.***Premaxilla–maxilla suture****, in dorsal view [C09m; O14m; S10m; Pb09m]*: **(0)** without constriction, with flat surface; **(1)** evident constriction.

15.***Maxilla*** *[A16; Z192m]*: **(0)** does not contribute to the orbit; **(1)** contributes to the orbit.

16.***Maxilla****, proportional number of neurovascular foramina relative to the number of teeth [A17m]*: **(0)** small number of foramina, usually 1–2 for each tooth; **(1)** greater number of foramina, widely surpassing the number of teeth.

17.***Maxilla****, distance between neurovascular foramina and teeth [A17m]*: **(0)** small distance, foramina positioned close to teeth; **(1)** foramina clearly apart from teeth.

18.*Inferior margin of the* ***maxilla*** *[W29; M24]*: **(0)** not different than the remaining surface from maxilla; **(1)** smooth surface, mesially inclined.

19.*Inferior margin of the* ***maxilla****, in lateral view [C79m]*: **(0)** concave at the anteriormost region and convex at the posteriormost region; **(1)** straight; **(2)** convex at the anteriormost region and convex and straight at the posteriormost region; **(3)** concave at the anteriormost region, convex at the midlength and concave at the posteriormost region, "festooned".

20.*Anterior border of the* ***nasals*** *[C13m]*: **(0)** short, at best with a small stiliform projection over the naris (eventually not in contact to the external naris due to isolation by the premaxillae); **(1)** moderately developed, projecting over the naris as a narrow lamina, without covering the naris; **(2)** well developed, completely covering the naris.

21.***Nasals****, general shape [A21]*: **(0)** triangular, posterior region wider than anterior region; **(1)** rectangular; **(2)** triangular, with the anteriormost region wider than the posterior region.

22.***Lachrymal*** *[C11; M05]*: **(0)** does not contact nasal, prevented by large contact among prefrontal–maxilla; **(1)** with small contact to nasal; **(2)** with large contact with nasal, preventing any contact among prefrontal–maxilla.

23.***Lachrymal*** *size [A23]*: **(0)** small; **(1)** well developed.

24.*Relative position of the anteriormost margin of the* ***prefrontal*** *[A25]*: **(0)** with anteriormost margin at the same relative position as the anteriormost margin of frontal; **(1)** anteriormost margin surpasses the anteriormost margin of frontal.

25.*Posterior margin of* ***prefrontal*** *[A26]*: **(0)** short, limited to anterodorsal border of the orbit; **(1)** elongated, composing the dorsal border of the orbit.

26.***Prefrontal pillars****, construction [C15m; S34m; Pb15m]*: **(0)** incomplete, without contact between the descending ramus of the prefrontal and palatine; **(1)** complete, with contact between the descending ramus of the prefrontal and palatine.

27.***Prefrontal pillars****, structure [C15m]*: **(0)** small contact area; **(1)** wide contact area.

28.***Frontal****, shape of anterior border [A28]*: **(0)** straight; **(1)** triangular to stiliform, projecting forward between nasals.

29.***Frontal*** *anterior border, suture [A29]*: **(0)** straight or with minor interdigitation; **(1)** strongly interdigitated.

30.***Interfrontal longitudinal ridge*** *[C22; A30]*: **(0)** absent; **(1)** present.

31.***Rostral transversal crest*** *[A31]*: **(0)** absent; **(1)** present.

32.***Frontal****, position of anterior border [A32]*: **(0)** between orbits; **(1)** at the same position that the anteriormost orbital border, in dorsal aspect; **(2)** positioned ahead of the orbits, in dorsal aspect.

Skull table (8 characters; 4.37% of total)

33.***Frontal*** *posterior border [C23; S20; M08]*: **(0)** short, with limited contact with the postorbital; **(1)** well developed, fairly contacting the postorbital and contributing to the supratemporal fenestra.

34.***Parietal*** *surface [C22m; M09m; S26m]*: **(0)** flat and wide; **(1)** flat, but narrow due to the development of the supratemporal fenestra; **(2)** sagittal crest.

35.*Anterolateral process of* ***postorbital*** *[C28; S24]*: **(0)** absent; **(1)** present.

36.***Supratemporal fenestra**, shape [A36m]*: **(0)** circular to subcircular; **(1)** elliptical, main axis clearly identifiable.

37.*External border of the **supratemporal fenestra**, orientation of the main axis in dorsal view [A37m]*: **(0)** diagonal, projection of the main axes converge posteriorly; **(1)** parallel, projection of the axes do not meet; **(2)** diagonal, projection of the main axes converge anteriorly.

38.*Proportional size of the **supratemporal fenestra** (main axis of the internal border) [C68m; S04m]*: **(0)** smaller than the diameter of the orbit; **(1)** subequal or bigger than the diameter of the orbit.

39.*Relation among the internal and external borders of the **supratemporal fenestra** [A39]:* **(0)** without significant difference; **(1)** external border slightly larger; **(2)** external border much larger.

40.*Area posterior to the **supratemporal fenestra**, where lies the parietal–squamosal suture [A40]*: **(0)** ample and flat horizontal surface; **(1)** surface extremely narrow and high, forming a crest transversal to the skull.

41.*Ventrolateral ramus of **squamosal**, in dorsal view [A41]*: **(0)** only slightly developed, suture with the quadrate covered by the superior lateral (temporal) ramus of the squamosal in dorsal view; **(1)** well developed, suture with the quadrate exposed in dorsal view.

TEMPORAL REGION (26 CHARACTERS; 14.2% OF TOTAL)

42.***Jugal** anterior ramus, shape in lateral view [S16m; M07m]*: **(0)** narrow throughout, widening directly at the contact with the maxilla; **(1)** gradually widening anteriorly; **(2)** sudden widening from the base of the ramus, “leaf–shaped”.

43.***Jugal** anterior ramus, external surface [A43; Z193]*: **(0)** well developed single neurovascular foramen, directed anteriorly to anterolateraly; **(1)** even surface, either flat or ornamented, without any kind or number of foramina; **(2)** two or more foramina, all small, facing ventrally.

44.***Jugal** anterior ramus, length [Pa134; Pb122; M29]*: **(0)** short, anteriormost margin does not reach the anterior margin of the orbit in lateral view; **(1)** long, either reaching or surpassing the anterior margin of the orbit in lateral view.

45.***Jugal** anterior ramus, relative position in lateral view [A45]*: **(0)** horizontal; **(1)** inclined diagonally, anterior border ventral to the base of the ramus.

46.*Jugal anterior ramus, occurrence of an external lateral crest [Pa133m; O145m; Pb121m]*: **(0)** absent; **(1)** present.

47.***Jugal** anterior ramus, cross–section [C18m]*: **(0)** circular to subcircular; **(1)** elliptical, with evident lateral compression.

48.***Jugal** posterior ramus [new]:* **(0)** straight; **(1)** dorsally arched.

49.***Postorbital bar**, relation to dermis [C25m]*: **(0)** subdermic, distinct, originating mesially from the jugal ramus; **(1)** dermic, gradually narrowing.

50.***Postorbital bar** [new]*: **(0)** straight; **(1)** posteroventrally bended at midlength.

51.***Postorbital bar**, constitution from ectopterygoid [C26m; S22]*: **(0)** does not receive contribution from ectopterygoid; **(1)** receive contribution from ectopterygoid.

52.***Postorbital bar**, ectopterygoid–postorbital contact [C26m; Pa158; O36; Pb144]*: **(0)** absent; **(1)** present.

53.***Postorbital bar**, general structure [C25m]*: **(0)** gracile; **(1)** robust.

54.***Postorbital bar**, inclination in lateral view [A54]*: **(0)** vertical; **(1)** diagonally inclined, distal end fairly anterior to the proximal end.

55.***Postorbital bar**, dorsal end next to the postorbital body [C30; S25]*: **(0)** bar gradually expanding towards the main body of the postorbital, without a well defined limit; **(1)** constriction delimiting the distinction between the postorbital bar and the postorbital body.

56.***Postorbital bar**, occurrence of vascular foramen on the lateral edge of the postorbital margin [C27; S23; T27]*: **(0)** absent; **(1)** present.

57.***Postorbital bar**, cross–section [C26; S21]*: **(0)** subcircular; **(1)** elliptical, with lateral compression.

58.***Postorbital bar**, implantation of the proximal end to the postorbital body [A58]*: **(0)** postorbital bar next to the laterodorsal border of the postorbital body; **(1)** postorbital bar next to the ventral portion of the postorbital body.

59.***Laterotemporal fenestrae** [O46]*: **(0)** facing laterally; **(1)** facing laterodorsally.

60.***Quadratojugal** mesial border, ornamentation of the posterodorsal margin of the laterotemporal fenestra) [S18m]*: **(0)** absent; **(1)** present, either ornamented with a discrete crest or a well defined spine (*Spina quadratojugalis*).

61.***Quadratojugal** anterodorsal ramus, development [C19m; S19m]*: **(0)** narrow and gracile; **(1)** wide and robust.

62.***Quadratojugal*** *anterodorsal ramus, contribution to postorbital bar [C19m; S19m]*: **(0)** does not contribute to postorbital bar; **(1)** contribute to postorbital bar.
63.***Quadratojugal*** *anterodorsal ramus, contact with postorbital bone [C19m; S19m]*: **(0)** contact posterior region of postorbital body; **(1)** contact anterior region of postorbital body.
64.***Quadratojugal****, contact with jugal [O39]*: **(0)** suture between jugal and quadratojugal lies next to the posterior vertex of the laterotemporal fenestra; **(1)** suture between jugal and quadratojugal lies below the laterotemporal fenestra, due to the development of a small process from the quadratojugal.
65.***Quadrate fenestrae*** *[C45m; S35m]*: **(0)** with no more than one fenestra; **(1)** with at least two well defined fenestrae.
66.***Quadrate****, surface [O154]*: **(0)** surface flat and even; **(1)** presenting one depression with triangular shape.
67.*Relative position of the* ***quadrate condyle****, in lateral/posterior views [W24m; S46m; Pb104]*: **(0)** at the same height than the occipital condyle, clearly above the teeth row; **(1)** below the occipital condyle, approximately at the same height of the teeth row; **(2)** clearly below the teeth row and the occipital condyle.
68.***Quadrate****, medial articulation facet of the condyle [O53]*: **(0)** small, with the same dimensions than the lateral articular facet; **(1)** large, bigger than the lateral articular facet, projecting ventrally.

BASICRANIUM (10 CHARACTERS; 5.47% OF TOTAL)

69.***Basisphenoid****, at the ventral portion of the skull [C56; S36; T56m]*: **(0)** exposed ventrally; **(1)** almost completely covered by the pterygoids and basioccipital.
70.***Basioccipital–quadrate contact*** *[new]*: **(0)** small or absent; **(1)** well developed, excluding the basisphenoid from the exoccipital and this last element from the ventral surface of the quadrate.
71.***Basioccipital*** *and* ***occipital condyle*** *[G32m; O176m; Pb112m]*: **(0)** facing posteriorly; **(1)** facing posteroventrally.
72.*Contact between* ***quadrate, squamosal*** *and* ***exoccipitals*** *[C49m; T49m; M14m]*: **(0)** without significant contact; **(1)** with well developed contact, lateral to cranioquadrate passage.
73.***Occipital surface****, in dorsal view [new]*: **(0)** overall flat; **(1)** "U–shaped", concave but flat in the area posterior to the skull table; **(2)** "V–shaped", exoccipitals posteromedially oriented from near the medial line.
74.***Exoccipital*** *surface, above the occipital crest [new]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.
75.*Insertion area for the m. depressor mandibulae, at the surface of* ***occipital*** *[A72]*: **(0)** slightly developed surface, narrow and low, smaller than the muscle attachment area of the exoccipitals; **(1)** well developed surface, with muscle attachment area similar to the surface of the exoccipitals.
76.*Lateral* ***occipital*** *surface of the squamosal [A73]*: **(0)** flat or slightly bended posteriorly; **(1)** strongly bended posteriorly, so the border is positioned posteriorly to the occipital condyle.
77.*External surface of the occipital portion of the* ***squamosal****, inclination [A74]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.
78.*Occipital surface of* ***supraoccipital****, inclination [A75]*: **(0)** faces posteriorly; **(1)** faces posterodorsally.
79.*Occipital surface of* ***supraoccipital****, in dorsal view [A76]*: **(0)** surface either flat and even or concave; **(1)** in "V", projecting posteriorly forming a vertically oriented medial ridge, or even a crest.

PALATE AND PERICHOANAL ELEMENTS (23 CHARACTERS; 12.57% OF TOTAL)

80.***Naso–oral fenestra*** *(=incisive foramen) [C07; O11–12m; S29; Pb07]*: **(0)** absent; **(1)** present, limited by the premaxilla; **(2)** present, limited by both the maxilla and premaxilla.
81.*Development of the palatine rami of the* ***maxilla*** *[C10m; S33m; Pb10m]*: **(0)** rami slightly developed; **(1)** rami well developed.
82.*Contact between palatine rami of the* ***maxilla*** *[C10m; S33m; Pb10m]*: **(0)** rami do not contact each other at the palate surface; **(1)** rami contact each other at the palate surface, eventually separated by vomer–palatine or vomer–pterygoids, but always forming a bony palate, separating nasal and oral cavities.
83.***Palatines*** *[C37; T37]*: **(0)** do not contact each other and do not contribute to a secondary palate; **(1)** contact each other, as part of the secondary palate.
84.*Bony surface of the* ***secondary palate*** *[O175; M47]*: **(0)** flat and even, or slightly convex; **(1)** concave.
85.***Maxillo–palatine fenestrae*** *[A82]*: **(0)** absent; **(1)** present.
86.***Suborbital fenestrae****, shape of anterior border [new]*: **(0)** rounded, smooth; **(1)** in sharp angle, forming a notch, fenestrae with the shape of a wide fissure.

87.***Suborbital fenestrae***, *composition of lateral border [O61m]*: **(0)** jugal takes part of the lateral border; **(1)** both ectopterygoid and maxilla compose the lateral border, excluding the jugal.
88.***Suborbital fenestrae***, *composition of anteromedial border [new]*: **(0)** composed exclusively by the palatines; **(1)** palatine ramus of the maxilla contributes to the anteromedial border, by means of a narrow and elongated process, directed posteriorly.
89.***Suborbital fenestrae***, *composition of posterior border [M35]*: **(0)** pterygoid takes part of the posterior border; **(1)** posterior border composed exclusively by the palatine and ectopterygoid, with pterygoid excluded by palatine–ectopterygoid contact.
90.***Palatine*** *anterior border [Z129]*: **(0)** do not exceed the anterior borders of the suborbital fenestrae; **(1)** clearly exceed the anterior border of the suborbital fenestra, directed anteriorly.
91.***Internal nares***, *shape, in palatal view [A87; Z195m]*: **(0)** anterior border usually straight or slightly arched, posterior border bended, with the overall shape of a reversed triangle; **(1)** slightly elongated, from rectangular or elliptical/ subcircular; **(2)** anterior border "V–shaped" due to the presence of posterolateral palatine processes (=palatine bar), posterior border straight or slightly bended, with the overall shape of a triangle.
92.***Internal nares***, *perichoanal crest delimiting at least the posterior border of the choanae [A88]*: **(0)** absent, borders smooth; **(1)** present.
93.***Internal naris*** *in adult specimens, orientation [A89m]*: **(0)** facing ventrally; **(1)** facing posteroventrally.
94.***Pterygoid*** *ventral rami, size [A90]*: **(0)** small; **(1)** well developed.
95.***Pterygoid*** *ventral rami, inclination [A91]*: **(0)** slightly inclined, posteroventrally oriented; **(1)** well inclined, ventrally oriented.
96.***Pterygoid*** *ventral rami, structure [A91]*: **(0)** gracile, with a laminar profile; **(1)** robust, thick.
97.*Fusion of the caudal portion of* ***pterygoids*** *[C41; O58; M12]*: **(0)** absent; **(1)** present.
98.***Ectopterygoid*** *medial process of the posterior ramus [A93; Z196m]*: **(0)** absent or incipient, ectopterygoid excluded from the internal naris by pterygoid–palatine contact; **(1)** present and well developed, contributing to the anterolateral border of the internal naris.
99.***Internal naris*** *anterior border [C44m; W59; S30m]*: **(0)** formed by either maxilla or palatines, in an anteriormost position, anterior to the suborbital fenestrae; **(1)** formed by palatines, text to the posterior margins of the suborbital fenestrae; **(2)** formed by pterygoids, positioned far posteriorly to the suborbital fenestra.
100.***Internal naris*** *posterior border [C44m; W59m; S30m]*: **(0)** maxillae or palatines; **(1)** pterygoids.
101.***Internal naris***, *length (compared to the length of suborbital fenestrae) [C42m; S31m]*: **(0)** clearly smaller than the suborbital fenestrae; **(1)** subequal in length.
102.***Interchoanal septum*** *[C69m; S32m; Pb69m]*: **(0)** absent; **(1)** present, laminar; **(2)** present, robust.
103.***Parachoanal fossae*** *[new]*: **(0)** absent; **(1)** present.

MANDIBLE (16 CHARACTERS; 8.75% OF TOTAL)

104.***Mandibular symphysis***, *length [O151m]*: **(0)** short, limited to the anteriormost portion of the rostrum, do not extend posteriorly further than the maxilla–premaxilla suture; **(1)** long, extending posteriorly beyond the maxilla–premaxilla suture, to a position below the 2nd–4th maxillary teeth.
105.***Mandibular symphysis***, *structure [W17; S44]*: **(0)** shallow, spatulated anteriorly; **(1)** deep.
106.***Mandibulary symphysis***, *contribution of splenials [C77; Pb77]*: **(0)** do not take part of the symphysis or at least do not take part with ventral exposure; **(1)** clearly take part of the symphysis, with ventral exposure.
107.*Disposition of* ***mandibulary rami***, *ant the anterior and middle sections [Pb155m]*: **(0)** mandibulary rami very close to each other, parallel; **(1)** mandibulary rami confluent, with a "V" or "Y" shape; **(2)** mandibulary rami parallel, but distant to each other, with the shape of a "U", forming an arch.
108.***Dentary***, *lateral aspect [A107]*: **(0)** anterior potion as deep as the posterior one; **(1)** dentary ramus gradually expand posteriorly, the posterior region been deeper than the anterior region; **(2)** dentary ramus suddenly expand posteriorly, the posterior region been deeper than the anterior region.
109.*Lateral surface of* ***dentary***, *at midsection [O81; M42]*: **(0)** flat, with lateral compression, with high lateral margin; **(1)** without lateral compression, lateroventral surface convex.
110.***Dentary*** *alveolar margin [W29m; M24m]*: **(0)** undifferentiated from the remaining dentary surface; **(1)** region flat and smooth, inclined mesially.
111.*Shape of the* ***dentary*** *alveolar margin, in lateral view [O84; S38]*: **(0)** straight or with a single elevation (if bearing an hypertrophied caniniform); **(1)** sinusoidal, undulated, with at least two concave regions and two tooth bearing elevations alternating to each other.
112.*Shape of anteromedial margin of* ***surangular*** *[C74; S41; Pb74]*: **(0)** straight, coronoid process absent;

(1) dorsally arched (coronoid process).

113.***Surangular*** *anterior border [new]:* **(0)** single or lightly furcated, directed to the lateral surface of the mandible; **(1)** clearly furcated and divergent, the medial ramus directed toward the splenial and the lateral ramus directed toward the dentary.

114.***Angular****, height of anterior ramus, in lateral view [C70; W18]*: **(0)** narrow; **(1)** high, excluding completely the posteroventral ramus of the dentary from the internal border of the maxillary fenestra.

115.***Angular****, length of the anterior ramus [A114]*: **(0)** short, not surpassing the anterior border of the mandibular fenestra; **(1)** moderately elongated, slightly surpassing the mandibular fenestra; **(2)** very long, reaching far beyond the fenestra.

116.***Prearticular*** *[C72; S39]*: **(0)** absent; **(1)** present.

117.*General proportions of* ***glenoid fossa*** *[W23m; M22m; S45; Pb103]*: **(0)** wider than longer or subequal; **(1)** longer than wider.

118.*Posterior border of the* ***glenoid fossa*** *[W23m]:* **(0)** posterior border even with the glenoid surface or, at best, incipient; **(1)** with a well developed posterior border, limiting anteroposterior movements from the mandible.

119.***Retroarticular process*** *[S47m]*: **(0)** posterodorsally oriented; **(1)** slightly developed or directed posteriorly; **(2)** posteroventrally oriented.

120.***Angular****, extension of the insertion area for m. pterigoideus posterior at the medial surface [C76; S42; P76]*: **(0)** absent; **(1)** present.

Dentition (28 characters; 15.3% of total)

121.***Teeth apex****, shape [A142]*: **(0)** apex usually rhomboid; **(1)** apex usually acute.

122.***Teeth apex****, inclination [A143]*: **(0)** without inclination or lingually inclined; **(1)** inclined posteriorly or posterolingually.

123.*Maxillary/dentary* ***posterior teeth****, surface [A126m]*: **(0)** smooth; **(1)** well striated by a great number of almost microscopic anastomosed ridges, with a general pattern from base to apex (but not exclusively); **(2)** macroscopic striation (base–apex), composed by gracile narrow ridges; **(3)** small number of robust ridges (base–apex), large and wide, similar to carinae, usually over the entire surface of the each crown.

124.*Total number of* ***premaxillary teeth*** *[W27m; O133m; Pb105m]*: **(0)** one; **(1)** two; **(2)** three; **(3)** at least four.

125.***Hypertrophied caniniform*** *at the premaxilla [A119]:* **(0)** present, without anterior teeth; **(1)** present, preceded by one tooth; **(2)** present, preceded by two teeth; **(3)** present, preceded by 3 teeth; **(4)** absent.

126.***Premaxillary*** **tooth** *posterior to the premaxillary hypertrophied caniniform [A120]:* **(0)** absent; **(1)** present.

127.*Distribution of* ***premaxillary teeth*** *[S74m]*: **(0)** over the whole alveolar surface of premaxilla; **(1)** edentulous region between premaxillary teeth, composing a medial diastema at the anteriormost region of the jaws.

128.*Premaxillary posteroventral extensions embracing partially or completely the base of the crown of the* ***first maxillary tooth*** *[new]:* **(0)** absent; **(1)** present.

129.*Total number of* ***maxillary teeth*** *[W30m; O164m; S51m; Pb107m]*: **(0)** no more than seven teeth; **(1)** no less than 10 teeth.

130.***Anterior maxillary dentition*** *[A124]:* **(0)** all maxillary teeth caniniform (subisometric and isomorphic); **(1)** hypertrophied caniniform preceded by 3–4 smaller teeth and followed by smaller caniniform teeth; **(2)** hypertrophied caniniform preceded by 1–2 smaller caniniform teeth and followed by smaller caniniform teeth; **(3)** hypertrophied caniniform, preceded by 1–2 smaller caniniform teeth and followed by smaller molariform teeth; **(4)** slightly enlarged molariform, preceded by 1–2 molariform–caniniform teeth and followed by molariforms; **(5)** all maxillary teeth molariform (subisometric and isomorphic).

131.*Area occupied by the* ***maxillary teeth****, in palatal view [A125]*: **(0)** proportionally small teeth, occupying only a marginal portion of the ventral surface of the maxilla; **(1)** proportionally well developed teeth, occupying large area the maxillary ventral surface (at least one third of the surface available).

132.*Mesial and distal surfaces of* ***maxillary teeth*** *[B104m; S53m]:* **(0)** heterogeneous carina, composed by anisomorphic tubercle–like denticles, developed preferentially at the posterior border; **(1)** either a smooth surface or a homogenous carina (crenulations may appear s a result of superficial ornamentation), extending over most of the anterior and posterior tooth surfaces; **(2)** homogenous carina, serrated with true denticulation (ziphodont dentition), extending over most of the anterior and posterior tooth surfaces.

133.*Implantation of* ***maxillary teeth*** *[P137]*: **(0)** not oblique; **(1)** oblique.

134.*Dental implantation at the* ***maxilla*** *(anterior and middle teeth) [O19m; M38m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

135.*Transverse section of posterior* ***maxillary teeth*** *[B116m; O104m; S52m; Pb140m]*: **(0)** strong lateral compression; **(1)** transverse section circular to subcircular, without significant lateral compression; **(2)**

transverse section 'teardrop–like' (=triangular), with asymmetric lateral compression occurring on the distal margin.

136.*Relative position of the* ***last maxillary tooth*** *[O18m; M37]*: **(0)** last tooth in anterior to the anteriormost border of the suborbital fenestra; **(1)** last tooth positioned posteriorly to the anteriormost border of the suborbital fenestra.

137.*Implantation of* ***posterior teeth at maxilla and dentary*** *[O18m; M38–39m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

138.*Occurrence of abrasion surfaces in* ***dentary and maxillary teeth*** *[A132]:* **(0)** teeth without abrasion surfaces due to masticatory action; **(1)** anteroposterior wear surface, indicating capacity for proal/propalinal movements of the mandible; **(2)** diagonal wear surface, indicating capacity for lateral movements of the mandible.

139.*Number of* ***dentary teeth*** *[A133]:* **(0)** no more than 10; **(1)** at least 11.

140.*Orientation of the* ***anterior dentary teeth*** *[A134]:* **(0)** vertical or subvertical; **(1)** mildly procumbent, anteriorly inclined; **(2)** strongly procumbent, anteriorly inclined, the first pair of teeth almost horizontal.

141.***Dentary symphyseal teeth battery*** *[new]:* **(0)** absent; **(1)** present, teeth from each pair closer to each other than to other teeth in the same hemimandible.

142.*Length of the* ***dentary teeth*** *occluding at the maxillary/premaxillary contact [C80; S54]*: **(0)** small to medium sized, subequal to other surrounding teeth; **(1)** hypertrophied, at least twice longer than surrounding teeth.

143.***Middle and posterior dentary teeth*** *(posterior to the maxillary/premaxillary suture) [C81m; O20m; S55m; Pb81m]*: **(0)** gradually bigger and than smaller, the same trait occurring with the occluding teeth at maxilla; **(1)** diminishing posteriorly; **(2)** gradually bigger and than smaller, the opposite occurring with the occluding teeth at maxilla.

144.*Implantation of the* ***middle and posterior dentary teeth*** *[new]*: **(0)** not oblique or slightly altered; **(1)** oblique (more than 30 degrees).

145.*Implantation of* ***middle dentary teeth*** *[O18m; M39m]*: **(0)** teeth set disposed in a groove, the roots originally isolated from each other only by soft tissue; **(1)** teeth set in isolated alveoli.

146.*Transverse section of* ***middle and posterior dentary teeth*** *[B116m; O104m; S52m; Pb140m]*: **(0)** strong lateral compression; **(1)** transverse section circular to subcircular, without significant lateral compression; **(2)** transverse section 'teardrop–like' (=triangular) to lozenge shaped, with asymmetric lateral compression occurring mostly on the anterior margin.

147.*Constriction at the crown–root transition, in* ***posterior maxillary and middle/posterior dentary teeth*** *[B117; S50; Pb157m]*: **(0)** absent; **(1)** present.

148.*Number of cusps of* ***posterior teeth*** *[G46m; B113m; Pb162m]:* **(0)** single apical cusp; **(1)** multicusped teeth, with two or more cusps.

149.*Lingual cingulus at the base of the crown of the* ***middle and posterior teeth*** *[A145]:* **(0)** absent; **(1)** present, with accessory cusps and styli.

Axial elements (16 characters; 8.75% of total)

150.***Cervical vertebrae*** *[C92; S57; P92]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic.

151.***Axis*** *centrum, length [A147]:* **(0)** centrum short, as long as high; **(1)** centrum clearly longer than higher.

152.***Axis****, neural spine laminae [Pb152m]*: **(0)** slightly developed, limited to the posterior half of the neural arch; **(1)** well developed over the whole extension of the neural arch due to the presence of prespinal and postspinal laminae, extending both anteriorly and posteriorly to the neural channel.

153.***Anterior cervical vertebrae****, neural spine laminae [C90m; Pb90m]*: **(0)** prespinal and postspinal laminae present; **(1)** laminae absent, neural spine rod–shaped.

154.***Anterior cervical vertebrae****, structure of neural spine [A151]*: **(0)** base narrow, gracile; **(1)** base short, wide, robust.

155.***Third cervical vertebrae*** *(CIII), development of prezygapophysis [A152]:* **(0)** slightly developed, projecting slightly anterior to the centrum; **(1)** well developed, clearly projecting anterior to the centrum.

156.***Posterior cervical vertebrae****, neural spine laminae [C90m; Pb90m]*: **(0)** prespinal and postspinal laminae present; **(1)** laminae absent, neural spine rod–shaped.

157.***Posterior cervical vertebrae****, structure of the neural spine [A153]*: **(0)** base narrow, gracile; **(1)** base short, wide, robust.

158.***Posterior cervical vertebrae****, development of the hypapophysis [Pb91m; W37m]*: **(0)** absent or slightly developed, no more than a sagittal ridge in the anterior portion of the centrum ventral surface; **(1)** present, well developed, laminar shaft projecting ventrally from the centrum anteroventral surface.

159.***Dorsal vertebrae**, development of the hypapophysis [A155]*: **(0)** absent or slightly developed, no more than a sagittal ridge in the anterior portion of the centrum ventral surface; **(1)** present, well developed, laminar shaft projecting ventrally from the centrum anteroventral surface.
160.***Dorsal vertebrae** [C93; S58; Pb93]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic.
161.***Caudal vertebrae** [C94m; Pb94m]*: **(0)** amphiplatyc or amphicoelic; **(1)** procoelic, the first vertebra eventually biconvex.
162.*Paramedian dorsal **osteoderms** (trunk) [C95; S61; Pb95]*: **(0)** wider than longer, rectangular; **(1)** as long as wide, with variable shape (square to subcircular); **(2)** longer than wider, elliptical.
163.*Anterolateral process developed at the anterior border of dorsal **osteoderms** [C96; S62; Pb96]*: **(0)** absent; **(1)** present.
164.*Number of **osteoderm** dorsal rows (trunk) [C97; S63; Pb97m]*: **(0)** two paramedial rows; **(1)** four rows, two paramedial and two accessory.
165.*Accessory **osteoderms** (trunk) [Pb97m]*: **(0)** absent; **(1)** present.
166.*Ventral **osteoderms** (trunk) [C100; S66; Pb100]*: **(0)** absent; **(1)** present.

APPENDICULAR ELEMENTS (16 CHARACTERS; 8.75% OF TOTAL)

167.*Anterior surface of **scapula** [C82; O120m; Pb82]*: **(0)** curved; **(1)** straight.
168.*Coracoid length, proportional to the **scapula** [C83m; S59m; Pb83]*: **(0)** much smaller, no more than half the length of the **scapula**; **(1)** smaller, approximately 60–75% of the length of the scapula; **(2)** subequal.
169.*Glenoid surface of **coracoid** extended on an oblique plane and the glenoid tip facing outwards and posteroventrally [O122m]*: **(0)** absent; **(1)** present.
170.*Styliform process of **coracoid** [O118]*: **(0)** absent; **(1)** present.
171.*Proximal head of **humerus** [O123]*: **(0)** facing backwards, posterodorsally; **(1)** facing dorsally, with a lateromedial major axis.
172.*Internal tuberosity at the proximal articulation of the **humerus** [O124]*: **(0)** slightly developed, with the articular surface dorsally oriented; **(1)** well developed, with articular facet ventral or oblique.
173.*Ligamentary depression at the surface of **humerus** [O125]*: **(0)** lateral to the internal tuberosity and below the proximal articulation of the humerus; **(1)** located laterally to the articulation of the proximal end of humerus.
174.***Humerus**, lateral aspect of the deltapectoral crest [O126]*: **(0)** convex; **(1)** concave.
175.***Ulna**, lateral compression [O168]*: **(0)** absent; **(1)** present at least at the distal end.
176.***Radial** [O127]*: **(0)** longer than wider; **(1)** length subequal to width.
177.***Radiale**, proximal end [Pb117]*: **(0)** symmetric, similar to distal articulation; **(1)** asymmetric, mesial exposure more representative than lateral.
178.***Ilium**, proportional length between the preacetabular and postacetabular processes [C84; S60; Pb84]*: **(0)** subequal; **(1)** postacetabular process clearly longer (approximately four times longer).
179.***Ilium**, orientation of the postacetabular process [W41; Pb110]*: **(0)** posteriorly or posteroventrally directed; **(1)** posterodorsally directed, positioned well above the preacetabular process.
180.***Ilium**, presence of the supracetabular crest [Pb116]*: **(0)** absent; **(1)** present.
181.***Femur** torsion [O149]*: **(0)** femur with light torsion, the difference in the orientation between the proximal and distal articulation facets approximately equals to 30 degrees; **(1)** femur with evident torsion, the difference in the orientation between the proximal and distal articulation facets approximately equals to 60 degrees.
182.***Femur**, position of the 4th trochanter [A178]*: **(0)** anteromedial; **(1)** posteromedial.
183.***Tibia**, proximal end [O87]*: **(0)** single concavity; **(1)** medial crest separating two concavities.

APPENDIX 3

Matrix used in the analysis. 20 terminals included, presented in alphabetical order, after the outgroups. 183 characters for each taxon. Characters grouped, with periods ('.') indicating clusters of 10; each line with 50 characters; periods not originally included in the matrix. Coding varies between 0–5; '?' = missing entries; '–' = inapplicable characters; '{ }' indicating variable condition of a character within the terminal.

Outgroup 1 – Sphenosuchia
0001101220.0101010020.021110?100.0212010101.0011000010.
0000001000.0000111000.1021111100.000??0000-.?0000?0000.
?00?100100.00?001011?.11?24?0012.1101011010.0010100000.
1100100000.?210000001.0100001000.001

Outgroup 2 – Protosuchia
0000101220.1?100??001.{01}{12}1110?000.01{01}201{01}001.0010000010.
0010001000.1?{01}0111000.1021110002.000100000-.?000010000.
?00?100100.00?0010110.????4??010.11010{01}1010.0110100000.
??00?00000.?010010001.0100001000.001

Alligatoridae
1111212{01}01.0210010030.1211111{01}{01}0.12000??010.1221101101.
1101110011.0011000010.0100000001.1110001101.0101101021.
0100101110.1000200101.10{12}3310011.0101110011.01?011{01}001.
1100111111.11011{01}1210.1011110110.110

Anatosuchus
0101210020.01000??002.0111110000.0000010010.0111101?0?.
0001????1?.001?001000.1?00?1001?.111000?001.10000?1011.
1100012100.00?110011?.10?34?1012.0101?110?0.00?01??00?.
??????????.??????????.??????????.???

Araripesuchus gomesii
1100111120.1101010031.1211111010.0210110010.0111101000.
1?01100110.0011001000.1100?1000?.1110001001.1000001011.
1101111110.00?1201011.11024?0012.010111?010.00?0110000.
?1????100.0010000200.01?01??1??.10?

Araripesuchus patagonicus
1100211120.1?01010021.12101??110.0210110010.0111101000.
??01100110.0011001000.1100100001.1110001001.1000001011.
0101?11110.00?1101011.11034?0012.010111?010.00?0110000.
?????????0.?0100?0??0.01001????1.1??

Baurusuchidae
0001002101.1?1101002?.?1111?1101.0101112111.0111{01}1100?.
0011100110.1101002100.1121111102.1110001?10.2011111111.
1111011001.01?1101121.1103210002.0201101000.0120110000.
?????????0.01?00??2?0.????11????.???

Bernissartia
1111212001.0211?10030.1??1111??0.0?0000?010.12?1101?0?.
11011100?1.0011????10.0100?????1.1110001??1.??01101?21.
0100111110.10??00100.0013310011.0101?1?01?.0?201?0000.
??00?11110.1001110?10.1011???1??.11?

Candidodon
0000110010.1010001112.?00?????0.0010010010.011?00100?.
??0110?110.??0?00??0?.1?11?1??10.111?0110??.10000?1011.
1101??1???.0?????????.000321?003.0101011???.??????101?.
?????????0.?1????????.????1?????.???

Chimaerasuchus
0??0100010.0111001101.0011??????.??????????.?????1????.
??????????.??????????.?????????2.01?1??????.??????????.
???100??0?.???1?010{12}1.1101100005.11011?110?.??1011?100.
0011?1110?.??0????10?.??????1101.???

Comahuesuchus
0010210000.0110?01122.01010??100.00?1?1?021.0100111?1?.
0001??????.??????2?00.112111110?.1110001110.201??1?011.
1??1112101.01?1??????.010?4??002.01?100?011.001?0??00?.
??????????.??????????.??????????.???

Crocodylidae
1111212{01}01.0211010030.?211111100.020000?010.1221101{01}01.
1101110011.0010000010.0100000001.1110001101.0101101021.
0100101110.1000200101.10{12}3310011.0101110011.0120110001.
1100111111.1101101210.1011110110.110

Malawisuchus
0000110110.0110101112.?210110000.02?0110010.00101000?0.
??0110?110.00010?2?00.101111?0??.111101100?.10000?1011.
0001011101.00?1001021.1{01}03210003.01010011?0.??10101110.
??11?11100.020??10???.????1?????.00?

Mariliasuchus
0100110000.0200101122.0?01010101.0111100021.0100101110.
0001101110.0001102100.111111101?.1110101010.2010011011.
1201011201.01110?1021.01122{01}0104.0010210102.001002100?.
00110110??.??????????.????1?????.???

Notosuchus
0100100020.1100?01122.0211010101.0111111011.0111100100.
0001101110.1?01102100.1111111011.1110101010.2010011111.
1201011201.01?11?1021.01?3300104.0?10210101.0010020000.
0011011000.00000?0100.01001111?1.001

Sebecus
0001012101.0111010021.1210111100.0101002010.0211101010.
1110101010.0011001000.11101?00?1.1111001101.10011?1011.
11010111?0.0000200101.11034?0011.0201001011.002010000?.
??????????.??????????.??????????.???

Simosuchus
0000211221.1200001112.2211110000.111110?021.021100?000.
0001101110.1110002100.1011111101.1101001001.?0?0?110??.
??00012001.01?1200121.00034?0015.0101001010.0010101100.
??11?11100.?2?101????.??????????.???

Sphagesaurus huenei
0000110000.1?00001112.?????10???.0??????0??.?001010000.
0001101110.0001????01.112??????2.11100010?0.201???1?11.
12?10?????.0?????????.0131011104.101121?2?1.1001?2100?.
?0????????.??????????.??????????.???

Thalattosuchia
0001112121.0200010010.021110?100.0112012100.0011000010.
0010001000.000000{12}000.0010101101.11100000??.10000?1011.
1001110110.00???10111.11?14?0010.0101111011.0010110000.
?100?00000.001001?2??.??????????.???

Uruguaysuchus
1000110020.1210110?22.00011??100.0110010010.?01000?000.
??01101110.??1?002000.1?11111101.111?00?001.1000011011.
11010111?1.00????0101.10032100?3.0?0?00?010.?0?0?0110?.
????????00.010?????00.101?1?0101.001

APPENDIX 4

Characters used by Zaher *et al.* (2006), and particularly referred in this analysis. Characters with a "+" were treated as ordered by Zaher *et al.* (2006). Characters labeled '**M**' are multistate, where order cannot be established between all or part of the states. Characters labeled '**X**' were excluded from the third step and substituted by a revised version in the fourth (final) step of the analysis, represented by a following number, also in bold.

Character 1 (modified from Clark, 1994; character 1). + External surface of dorsal cranial bones: smooth (0), slightly grooved (1), and heavily ornamented with deep pits and grooves (2). **M**

Character 3 (modified from Clark, 1994; character 3). + Rostrum proportions: narrow oreinirostral (0) or broad oreinirostral (1) or nearly tubular (2) or platyrostral (3). **M**

Character 65 (modified from Clark, 1994; character 65). + One small palpebral present in orbit (0) or one large palpebral (1) or two large palpebrals (2). **M**

Character 67 (Clark, 1994; character 67). + Antorbital fenestra: as large as orbit (0) or about half the diameter of the orbit (1) or much smaller than the orbit (2) or absent (3). **M**

Character 105 (modified from Wu & Sues, 1996, and Ortega *et al.*, 2000; character 27 and character 133, respectively). + Premaxillary teeth: five (0), four (1), three (2), or two (3). **M/X-200, 202**

Character 107 (modified from Wu & Sues, 1996; character 30). + Maxilla: with eight or more teeth (0) or seven (1) or six (2) or five (3) or four (4) teeth. **M/X-201, 202**

Character 120 (Ortega *et al.*, 1996, 2000; characters 11 and 100, respectively). Tooth margins: with denticulate carinae (0) or without carinae or with smooth or crenulated carinae (1). **X-204**

Character 143 (Pol, 1999a; character 157). + Postorbital process of jugal: anteriorly placed (0), in the middle (1), or posteriorly positioned (2). **M**

Character 192 (original from Zaher *et al.*, 2006). Ventral half of lacrimal: extending posteroventrally, widely contacting the jugal (0) or tapers posteroventrally, not contacting or contacting slightly the jugal (1). **X-203**

Character 193 (original from Zaher *et al.*, 2006). Large foramen on lateral surface of anterior jugal: absent (0) or present (1). **X-199**

Character 194 (original from Zaher *et al.*, 2006). Procumbent premaxilary and anterior dentary alveoli: absent (0) or present (1). **X-205**

APPENDIX 5

Characters included in the modified matrix from Zaher *et al.* (2006), translated and adapted from Andrade (2005).

Character 199 [Andrade, 2005 (43); mod. Zaher *et al.*, 2006 (193)]. Ventrolateral surface of anterior ramus, near its contact with the maxilla: smooth or ornamented surface, without the development of neurovascular foramina (0) or single well-developed neurovascular foramen, anteriorly directed (1) or two or more neurovascular foramina, ventrally oriented (2).

Character 200 [mod. Wu & Sues, 1996 (*27*); mod. Ortega *et al.*, 2000 (*133*); mod. Zaher *et al.*, 2006 (*105*)]. Teeth supported exclusively by the premaxilla: five (0), four (1), three (2), or two or one (3).

Character 201 [mod. Wu & Sues, 1996 (*27*); mod. Zaher *et al.*, 2006 (*107*)]. Number of teeth supported entirely by the maxilla: eight or more teeth (0) or seven (1) or six (2) or five (3) or four (4) teeth.

Character 202 [mod. Andrade, 2005 (*122*)]. Intermediate tooth at the upper series, partially supported by the maxilla posteriorly and by posterior extensions of the premaxilla, anteriorly: absent (0) present (1).

Character 203 [mod. Andrade, 2005 (*16*); mod. Zaher *et al.*, 2006 (*192*)]. Maxilla: is excluded from the orbit by lachrymal-jugal contact (0) or reaches the anteroventral border of the orbit, preventing lachrymal-jugal contact (1).

Character 204 [mod. Ortega *et al.*, 1996 (*11*), 2000 (*100*); mod. Andrade, 2005 (*126*); mod. Zaher *et al.*, 2006 (*120*)]. Teeth margins: at least anterior and medial teeth with a homogeneous denticulate carinae, composed of true blade-like ziphodont denticles (0), or all teeth smooth or with a homogeneous crenulated false-ziphodont carinae (1) or anterior dentition smooth and medial/posterior teeth with heterogeneous denticulated carinae composed of tuberous and romboid denticles (2).

Character 205 [mod. Zaher *et al.*, 2006 (*194*)]. Premaxilary and anterior dentary alveoli: procumbent, with well-developed curved caniniform teeth (0), mostly vertical, with curved caniniform teeth (1) or procumbent, with small to medium incisiform teeth (2).

APPENDIX 6

Character entries for revised taxa, used in the modified matrix of Zaher *et al.* (2006). States in bold represent changes in the original matrix (1-198) or characters added in this analysis (199-205). Characters grouped, with periods ('.') indicating clusters of 10; each line with 50 characters; periods not originally included in the matrix.

*Notosuchus*NEW
101?001101.0**0**00111000.1111110011.0001022110.1100211120.
11?1000010.?110211111.2?01011100.01{01}111?1?2.00001000??.
0122011???.1100101**0**11.01**1**01001**1**0.**1**0001**0**1111.1**0**11?00011.
1100100001.01**?**1011000.0111011000.0000000000.00001111**01.21022**

*Comahuesuchus*NEW
103??0?101.??00?????0.112???????.?0010?2???.?1?011?1??.
??????????.?????131??.???**1**0?1010.1?????????.??????????.
????{01}13???.1??????0?1.0**1**1**1**1201**1**0.1?????011?.?0?1????11.
???11?0010.0?1?0??000.???100??0?.000??0????.011110?1**1?.30112**

*Mariliasuchus*NEW
101?00**0**101.0000111000.1(01)**1**1110001.1001022110.100**0**21?120.
11?1000010.?1?0213111.210**1**0?1100.0????????**2.00**????????.
??22111???.11?????0**1**1.0**1**101001**1**?.1100{01}0**(01)**111.10110?0011.
1100110001.00110**1**1000.01?1010000.0000000???.011110?1**12.31122**

*Candidodon*NEW
?**01**??**0**??**01**.??**00**??**11**??.???**11**?????.??????**2**???.??**00**??????.
??????**0**???.????**(12)1**?**1**??.???????**11**?.??????????.??????????.
???**(12)**?**11**???.?????????1.??????????.??????0??**1**.??**1**???????.
???**0**?1?**0**??.2??????**0**??.????????**00**.??**000**?????.**0000**????**0?**.**10011**

*Sphagesaurus*NEW
101?000101.??00??100?.????110???.??????2110.1?00?????0.
11?1000???.?????13?2?.???????100.**0**???????1?.??????????.
????312???.?0???????1.1111101111.11111**0**1111.10**1**1110111.
1?0**0**11?0??.011?0**1**10??.01??000000.?00???????.00**10111113.3?022**

*Uruguaysuchus*NEW
201?001101.??00??10??.1??1????1?.??01022?10.1?0011????.
1?????0??0.???01111(12)?.??00011010.0??1?1????.??0000?0??.
01?2100210.0?00?000?{01}.???01?1?00.????1?0111.?11????11.
?????1?000.1????????0.???10?????.00????????.0**1**????1?**?1.00111**

*Malawisuchus*NEW
101?00?111.0000?(01)1000.1(01){01}1100?11.0001?22110.100011??20.
???1000?10.?1?02?111(01).2?01011100.01????1??2.10000010??.
01(12)2111???.01?0???011.00101?1100.0???110110.101?0?0001.
???0?100??.21110?1000.0111000000.0000000???.0**1**?00?10**?1.10111**

*Aragomesii*NEW
2010001101.0000111000.1011111011.(01)001022110.1000111120.
11?10000?0.?110201121.210001101{01}.{01}1{01}11111?1.{234}000100010.

0111100210.010010101**1**.0100100100.0000100110.0021000011.
0?0011{01}000.0111101000.011100?000.0000000000.0?000?10**01**.**00011**

*Arapatagonicus*NEW
201000?101.0000?1{01}000.101111?011.1001022?10.100011?12?.
11?1000??0.?1?02?1121.2?0?011{01}1?.?1?1??????.????1000??.
0111100???.01???0?01**1**.01101?0100.00??100110.102?0??01?.
???0??{01}100.0111?01000.01110?0000.0000000000.0?000?10**01**.**00011**

APPENDIX 7

Additional matrix entries for added characters (199-205), used in the phylogenetic analysis based on a modified version of matrix by Zaher *et al.* (2006). Periods ('.') indicate the 200th character, but not originally included in the matrix.

Gracilisuchus	?2.00?01	*Lomasuchus*	0?.00?0?
Terrestrisuchus	??.00?0?	*Peirosaurus*	?0.00?01
Dibothrosuchus	00.00?01	*Theriosuchus*	?0.00?1?
Protosuchus	01.00001	*Alligatorium*	??.?????
Hemiprotosuchus	??.00001	*Goniopholis*	00.00?1?
Orthosuchus	?1.40011	*Eutretauranosuchus*	00.00?1?
Kayenta	?1.20?1?	*Pelagosaurus*	??.00?1?
Zaraasuchus	??.?????	Teleosauridae	?1.00?1?
Gobiosuchus	02.00?11	Metriorhynchidae	?2.00010
Sichuanosuchus	01.00011	*Sokotosuchus*	??.???1?
Shantungosuchus	??.???11	Dyrosauridae	??.??010
Zosuchus	02.30?11	*Pholidosaurus*	??.??01?
Fruita	??.00?1?	*Bernissartia*	?0.0001?
Hsisosuchus	0?.00001	*Hylaeochampsa*	??.???1?
Chimaeresuchus	03.40012	*Borealosuchus*	?0.00?1?
Simosuchus	00.00011	*Gavialis*	20.00010
Bretesuchus	?1.0000?	*Crocodylus*	20.00010
Baurusuchus	?1.30001	*Alligator*	20.00010
Iberosuchus	0?.???01		

APPENDIX 8

Command lines for PAUP used in the phylogenetic analysis, shown under brackets.

Sets the use of simplest optimization between ACCTRAN and DELTRAN:
[pset opt=minf;]

Exclude character 5, due to redundance in the matrix, as in Pol (2003) (steps 1-3):
[exclude 5;]

[Exclude revised characters (step 1):
[exclude 199 200 201 202 203 204 205;]

Exclude selected characters (steps 2-3):
[exclude 105 107 120 192 193 194;]

Excludes from the analysis taxa as coded in this study (step 1):
[delete *Notosuchus*NEW *Comahuesuchus*NEW *Mariliasuchus*NEW *Candidodon*NEW *Sphagesaurus*NEW *Uruguaysuchus*NEW *Malawisuchus*NEW *Aragomesii*NEW *Arapatagonicus*NEW;]

Excludes from the analysis taxa as originally coded (steps 2-3):

[delete *Notosuchus Comahuesuchus Mariliasuchus Candidodon Sphagesaurus Uruguaysuchus Malawisuchus Aragomesii Arapatagonicus*;]

Order characters as originally used by ZAHER *et al.* (2006):
[ctype ord: 1 3 6 23 37 45 49 65 67 69 73 77 79 90 91 96 97 103 104 105 107 126 143 149 165;]

Order characters - reduced list (steps 1-2):
[ctype ord: 6 23 37 45 49 69 73 77 79 90 91 96 97 103 104 126 149 165;]

Order characters according to reduced criteria, including new characters (step 3):
[ctype ord: 6 23 37 45 49 69 73 77 79 90 91 96 97 103 104 126 149 165 204 205;]

NOTE ADDED IN PRESS:

After the conclusion of this manuscript, NOBRE *et al.* (2007; see references) described a new species, *Mariliasuchus robustus*, which is not mentioned in this paper. However, the holotype of the new species (UFRJ-DG-56-R) is cited and included in the range of the specimens of *M. amarali*. The existance of two or more species of *Mariliasuchus* does not preclude the classification of this genus in Notosuchidae or hinders the intergeneric comparisons presented here. However, the matter is relevant to the intraspecific variability of *M. amarali*. We understand that: (i) the poor preservation of the holotype (as discussed in this paper) does not allow a secure diferentiation of the specimen UFRJ-DG-56-R from *M. amarali*; (ii) robustness itself cannot support the recognition of a different species; (iii) the diagnosis presented by NOBRE *et al.* (2007) lacked convincing autapomorphies to support *M. robustus*, and no distinctive characteristic was provided to support the distinction of *M. amarali* from *M. robustus*. Until new evidence arrises and further work is produced to understand the variability of *Mariliasuchus*, a conservative approach is preferred. Therefore, UFRJ-DG-56-R is here considered as part of *M. amarali*.